University of Alberta

Post-fire dynamics of the boreal forest floor: measurement and modelling of long-term carbon accumulation in upland forests

by

Ian A. Nalder ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Doctor of Philosophy

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Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Post-fire dynamics of the boreal forest floor: measurement and modelling of long-term carbon accumulation in upland forests submitted by Ian A. Nalder in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Forest Biology & Management.

Dr. Ross W. Wein, Supervisor

Dr. Michael J. Apps

Robert Grant

Dr. Robert F. Grant

for

Dr. Seppo Kellomäki, External Reader

Dr. William B. McGill

DW Schindler

Dr. David Schindler

Dr. Francis C. Yeh

26 August 2002

Dedication

To my wife, Sue, who shared it all and contributed so much

Abstract

Forest floor carbon (FFC) dynamics over the life of a stand, and the consequent climate change implications, are investigated through a literature review, field sampling of six chronosequences and computer simulation. The six chronosequences, encompassing 80 forest stands, were based on two tree species, *Pinus banksiana* and *Populus tremuloides*, in each of three climatic zones in the western Canadian continental boreal forest. To aid this study, a novel corer for efficient forest floor sampling was developed, as well as a new interpolation technique to estimate climatic variables for each of the 80 sampled stands. For the simulations, two existing patch models using different approaches were tested (FORSKA2V and BORFOR), but both gave poor results and had inherent flaws for this region. Instead, a carbon input-output model was developed based on the decay algorithms of CENTURY and litter inputs that were defined by regressions of tree, shrub and moss data from the chronosequences.

The forest floor was a major, labile store of organic carbon, as well as being an important control of nutrient cycling and soil thermal and moisture regimes. To examine FFC dynamics, it was hypothesized that FFC was related to stand age, species and climate. The field study found that there was a difference between species, and that stand age and climate affected *P. tremuloides* FFC but not that of *P. banksiana*. Because of these effects, FFC storage was expected to be sensitive to a changing climate due to direct climatic effects as well as altered disturbance intervals and changes in species distribution. The model supported the hypothesized age and species effects, but climatic effects were not evident. To resolve discrepancies between observed and simulated patterns, and to allow for model improvements, there is a need to understand controls on shrub and moss/lichen growth, to better quantify litter from logs and fine roots, and to confirm appropriate decay rates for forest floor materials. It is concluded that the forest floor is an important store of carbon that will be sensitive to a changing climate, although improved models will be required to quantify such changes.

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1. The role of forest floors in boreal regions: implications for climate change

Introduction

Northern ecosystems are increasingly recognized as playing an important role in climate change (IPCC, 2001; Woodwell et al., 1998). Boreal forests in particular have the potential to form an important biotic feedback. These forests store such large amounts of carbon, estimated at 709 gigatonnes (Apps et al., 1993), that relatively small changes can have substantial impacts on atmospheric carbon. For example, a carbon loss of just 0.1% per year from boreal forests is in line with the 0.8 GtC yr^{-1} postulated by Kasischke et al. (1995). This would represent a 21% increase in the contemporary buildup rate of atmospheric carbon, estimated to be 3.3 GtC yr^{-1} (Schimel et al., 1996). Such a change could be expected to increase radiative forcing and affect climate. At the same time, carbon pools are sensitive to climate, particularly temperature (Kauppi et al., 1997; Liski and Westman, 1997) and temperature increases in boreal regions are likely to be relatively large, according to projections of general circulation models (GCM's) (Kattenberg et al., 1996). The potential for climate change feedbacks is clear, but their magnitude and sign remain uncertain.

The forest floor is a vital component of forests (Pritchett and Fisher, 1987), particularly boreal forests (van Cleve and Noonan, 1975). It is defined as the layer of mainly detrital material on top of mineral soil, comprising litter, ferment and humus layers (Kimmins, 1987; Pritchett and Fisher, 1987). These layers correspond to the Oi, Oe and Oa horizons in the American system (Soil Survey Staff, 1981) and the L, F and H horizons in the Canadian system (Agriculture Canada Expert Committee on Soil Survey, 1987). Another commonly used terminology divides the forest floor into litter and duff layers. Where present, moss is intimately associated with the forest floor, and is sometimes referred to as part of the forest floor (e.g., Sharratt, 1997); strictly live moss is a separate layer, and it is treated as such here. Forest floors occur in upland forests as distinct from peatlands which are dominated by high water tables and have organic horizons deeper than 30 or 40 cm (Gorham, 1991).

In boreal forests there is little of the faunal activity that in more southerly regions mixes organic and mineral soil horizons. Consequently, the forest floor usually forms a distinct layer with an abrupt transition to the underlying mineral soil. Nevertheless, the forest floor is heterogeneous. It comprises litter inputs from foliage, seeds, branches and stems from a variety of plant species with a continuum of decay states and intermixed with fine roots, mycorrhizae, exudates, bacterial biomass, fungal hyphae, as well as small amounts of mineral soil and charcoal. Such heterogeneity gives special problems in understanding forest floor responses to a changing climate. This understanding is critical, because as will be shown, the forest floor is a key mediator of many processes that control tree growth as well as being a significant carbon store in its own right. Despite this, it remains a relatively unexplored research area. A review of abstracts of 600 boreal forest papers published in 1997 and 1998 found that only 4% were devoted to the forest floor layer compared with 37% devoted to the tree or canopy layer (Figure 1-1). Not surprisingly, there are many unresolved issues which prevent adequate assessments of the impacts of climate change.

The objectives for this chapter are to provide a review of the characteristics and role of the forest floor, to highlight its importance for climate change predictions, and to identify key areas where further research is needed.

Major characteristics of the forest floor

Forest floors vary greatly across forest stands, depending on age, climate, topography, vegetation, and successional status. Characteristics may be relatively uniform within a stand, yet there is still considerable spatial variation: coefficients of variation of about 30% are common (e.g., Grigal et al., 1991; Liski, 1995; Nalder and Wein, 1998). Nevertheless, its characteristics clearly set it apart from the underlying mineral soil. Most obvious is its unique physical character. It is fibrous, often matted with fungal hyphae and fine roots, has an extremely wide range in size and hardness of particles, and mineral soil particles are nearly always a significant component. Such physical heterogeneity, combined with high spatial variability, creates special challenges for sampling (Nalder and Wein, 1998), analysis and interpretation of data. Surface organic depths usually range from 1 to 25 cm, and the organic matter content, at typically 20-80%, is an order-of-magnitude greater than mineral soil.

The high organic matter concentration has important implications. First, the forest floor may store as much or more carbon and mineralisable nutrients than active horizons of the mineral soil. Second, oven-dry bulk densities are about an order of magnitude lower than the underlying mineral soil (Figure 1-2). Forest floor values generally range from 0.05 - 0.2 Mg m^{-3} (van Cleve et al., 1981; Alban, 1982; Liski and Westman, 1995; Sharratt, 1997; Nalder and Wein, 1998). This low bulk density leads to a relatively high moisture storage capacity. Few data exist for forest floors, but a generalized value for available water holding capacity (i.e., field capacity minus wilting point) is 35% by volume (Bonan, 1989). In contrast, coarse-grained mineral soils examined in the western Canadian boreal forest had values as low as 1% and even fine-textured soils seldom exceeded 20% (Nalder, unpublished data). Low bulk densities of forest floors also provide higher thermal insulating capacities than mineral soil. For instance, thermal conductivities of dry and wet peat are 0.06 and 0.50 W m^{-1} K^{-1} compared with 0.25 and 1.58 W m^{-1} K^{-1} for dry and wet clay, respectively (Table 2.1 Oke, 1987). It should be noted that data are scarce and that thermal conductivities for peat are likely an overestimate of forest floor values, e.g., in-situ values in a *Picea mariana* stand vary from 0.03 to 0.09 W m^{-1} K^{-1} over a growing season (Sharratt, 1997).

Considerable data exist for chemical characteristics of the forest floor. Detailed nutrient data are available for a wide range of sites (van Cleve and Noonan, 1975; MacLean and Wein, 1977; Gordon, 1983; van Cleve et al., 1983a; Green et al., 1993; Klinka et al., 1994; Huang and Schoenau, 1996; Trofymow and CIDET Working Group, 1998; Schwendenmann, 2000) and again there are considerable differences from mineral soil. C:N ratios decline with depth, with the litter layer having wide ratios typical of fresh litter and mineral soil horizons approaching the narrow ratios of microbial biomass (Figure 1-3); thus forest floor C:N ratios usually range from 20 to 60 while mineral soil values from 10-20 are more common.

Boreal forest floors are also generally acid, with pH values of 3-5 and 5-7 commonly recorded in coniferous and deciduous stands, respectively. Underlying mineral soils tend to have higher values (e.g., Figure 2 Alban, 1982). This low pH leads to the decomposer community being dominated by fungi (e.g., Figure 7 Wagener and Schimel, 1998): thick fungal hyphal mats are common, and fungal biomass is strongly related to forest floor organic matter and decay rates (Flanagan and van Cleve, 1983). The forest floor is also much more labile than mineral soil. Forest floor turnover times typically range from 5 to 100 years (van Cleve and Noonan, 1975; MacLean and Wein, 1978; van Cleve et al., 1981; Perala and Alban, 1982; Flanagan and van Cleve, 1983; Weber, 1987; Gower et al., 1997), whereas mean turnover times for carbon in boreal mineral soils range from centuries to millenia (Harden et al., 1992; Goulden et al., 1998).

Roles of the forest floor

Carbon pool

Globally, boreal forests store an estimated 709 PgC (Apps et al., 1993), approximately one third of the 2,190 Pg of organic C in terrestrial ecosystems (Schimel, 1995). About 40% of boreal forest carbon is in upland forests (from data in Apps et al., 1993). To assess the magnitude and relative importance of the forest floor, data from many studies are summarized in Table 1-1. There is considerable variation, arising from differing definitions and methodologies as well as from actual differences between regions and sites. Nevertheless, it is clear that the forest floor is a significant carbon pool. Measurements range from 1.1 to 7.0 kgC m^{-2} and in some cases exceed the aboveground pool. Mineral soil pools generally dominate, with estimates ranging from 1.4 to 15.8 kgC m^{-2}, but are probably less important for climate change because their dynamics are measured over centuries or millennia (Protz et al., 1984; Protz et al., 1988; Schlesinger, 1990; Harden et al., 1992; Liski et al., 1998). In contrast, forest floor dynamics occur over the intervals between disturbances, usually measured in decades, which are comparable with the timescales of interest for predicting climate change impacts.

Forest floor dynamics, however, are poorly known. The forest floor is partially or completely removed by disturbances, principally fire, after which the forest floor rebuilds at a rate dependent on the balance between litter input and decomposition. It must be stressed that this is a delicate balance because the inputs and outputs are large compared with the net annual change. Forest floor biomass may or may not reach steady state before the next disturbance. Several studies provide evidence for long-term forest floor or humus accumulation (Stoeckeler, 1961; Heinselman, 1973; van Cleve and Noonan, 1975; Bradshaw and Zackrisson, 1990; Morrison et al., 1993; Paré et al., 1993; Gorshkov et al., 1996; Harden et al., 1997; Wardle et al., 1997). Several other studies have found no effect of age or suggest that equilibrium is reached within a decade or two (MacLean and Wein, 1977; Paré and Bergeron, 1996; Krause, 1998). In the short term, the post-disturbance residual forest floor may initially decline (e.g., Federer, 1984; Krause, 1998; Slaughter et al., 1998) because of reduced litterfall and conditions that favour increased decomposition rates. It is often assumed that the forest floor is at steady state for the purposes of calculating turnover times (van Cleve and Noonan, 1975; MacLean and Wein, 1978; van Cleve et al., 1981; Perala and Alban, 1982; Flanagan and van Cleve, 1983; Weber, 1987; Gower et al., 1997), for carbon and nitrogen budgets (e.g., Raich and Nadelhoffer, 1989; Gower et al., 1996; Gundersen et al., 1998), or for fire behaviour predictions (Forestry Canada Fire Danger Group, 1992). The validity of this assumption is open to question. Actual dynamics at a specific site are likely dependent on species and climate, both of which affect productivity and decay, but much more research is required to predict this dynamic with any certainty.

Soil microclimate regulation

As previously outlined, the forest floor has very different characteristics to mineral soil. Consequently, the presence of the forest floor can alter soil microclimate. The low conductivity results in slow warming of underlying soils in spring and leads to low summer soil temperatures. Low soil temperatures can reduce productivity through a variety of mechanisms (Bonan, 1992) and thick forest floors are usually associated with low productivity in cold regions (van Cleve and Yarie, 1986). The low soil temperatures also have implications for carbon budgets because summer decomposition is retarded. Conversely, winter decomposition, which can be significant (Moore, 1983; Pajari, 1995; Goulden et al., 1998), may be higher because soil temperatures are moderated by thick forest floors, although the insulation provided by snow packs is generally the dominant influence. The low thermal conductivity of the forest floor also gives high surface temperatures when exposed to solar radiation which has implications for seedling establishment (see Regeneration section). The forest floor adds considerably to the water holding capacity of the soil system because of its high moisture storage and stratification effects; it also reduces evaporation from underlying mineral soil and reduces adverse effects of rainfall such as runoff, rain drop erosion and puddling (Pritchett and Fisher, 1987). Consequently, the presence and characteristics of the forest floor can be expected to have a large effect on soil microclimate.

Rooting zone

In boreal regions, mean annual air temperatures generally range between 2 and -6 degrees which results in low summer soil temperatures at depth (e.g., Viereck, 1970; Yin and Arp, 1993; Schulze et al., 1995; Huang and Schoenau, 1997b; Goulden et al., 1998; Russell and Voroney, 1998) and shallow permafrost in some areas. Consequently, the upper layers are more biologically active and roots, particularly fine roots, are concentrated near the soil surface (Jackson et al., 1996). This is evident with many species. In *Picea mariana*, the forest floor is the principal zone for tree rooting (van Cleve et al., 1981). In a *Picea abies* stand, the organic layer contains 328 g m^{-2} root biomass versus 103 g m^{-2} in mineral soil horizons (Gundersen et al., 1998). In two *Pinus sylvestris* stands, three-quarters of fine root biomass is in the F/H layer with biomass declining exponentially with depth (Persson, 1980). Strong and La Roi (1983) report maximum root concentrations in the LFH layer and close linear relationships between the logarithm of root concentration and root depth for several *Pinus banksiana*, *Populus tremuloides* and *Picea mariana* stands in Alberta. Similar patterns are reported in later studies (Ruark and Bockheim, 1987; Finer et al., 1997; Huang and Schoenau, 1997b). Clearly the forest floor forms a very important rooting zone for trees.

Nutrient storage and cycling

Root distribution is reflective of the role of the forest floor in nutrient recycling and its importance has been highlighted by many studies (MacLean and Wein, 1977; MacLean and Wein, 1978; Chapin III, 1983; Flanagan and van Cleve, 1983; Gordon, 1983; van Cleve et al., 1983a; Chapin III, 1986; Weber, 1987; Foster et al., 1995; Huang and Schoenau, 1997b). Litter settles on the forest floor where it is broken down and decomposed by soil fauna, micro-organisms and fungi. Nutrients such as N, P and S are mineralized and taken up by plants, and may also be taken up directly in organic form (Carleton and Read, 1991; Schulze et al., 1994; Näsholm et al., 1998). In either case, plants recover and recycle much of the nutrients lost in litterfall. The forest floor has four characteristics that make it attractive as a nutrient source: first, it is usually a large store of organic matter (Table 1); second, this organic matter is concentrated in a relatively thin layer; third, turnover times provide a gradual release of nutrients at a rate commensurate with plant requirements; and fourth, it can intercept nutrients that enter the system in precipitation and throughfall because of its high water holding capacity and the fact that the water must pass through the forest floor to reach mineral soil. Though little recognized, it appears that the forest floor also has a significant role in fixing atmospheric nitrogen (Wei and Kimmins, 1998), which may have considerable importance in nitrogen-limited boreal forests. In summary, the forest floor is critical for plant nutrition.

Fire fuel load

Forest fires require a continuous layer of dry, fine fuel on the ground to be able to spread (Van Wagner, 1983). In dry conditions, the forest floor and moss/lichen layers meet these requirements and become key fuels (e.g., see Table 6 Volokitina, 1996). They not only allow the fire to spread but also affect fire intensity and rate of spread. Consequently, the characteristics of the forest floor are important for predicting forest fire behaviour (Forestry Canada Fire Danger Group, 1992; Keane et al., 1996). The spreading front tends to remove the surface litter, but the rest of the forest floor becomes fuel for smouldering combustion (Van Wagner, 1983). Relative to the fire front, smouldering combustion spreads very slowly and may cause re-ignitions and holdover fires, particularly in deep organic deposits (Wein, 1983; Frandsen, 1997). Fire severity may be classified according to the amount of forest floor removed (Viereck and Schandelmeier, 1980), but this is one of the least known aspects of fire behaviour although it has considerable implications for carbon budgets and regeneration.

Regeneration

Regeneration is critically dependent on the amount of forest floor removed by fire. If the forest floor remains largely intact, its low thermal conductivity protects buried propagules from lethal temperatures; conversely, deep burning fires will tend to consume propagules in the forest floor and may kill those buried in mineral soil (Johnson, 1992). However, removal of the forest floor provides an improved seedbed because most boreal tree species regenerate better on exposed mineral soil (Zasada, 1986; Johnson, 1992). For seeds, temperature and availability of moisture are probably key limitations because forest floor surfaces reach high temperatures and dry rapidly when exposed to the sun. For vegetative regeneration, forest floor effects on microclimate can also be important, e.g., *Populus tremuloides* root suckering is inhibited at temperatures less than 15 °C (Maini, 1967) and low soil temperatures are associated with thick forest floors. But many other effects may be important. Evidence is emerging that charcoal in the forest floor may promote regeneration through adsorption and inhibition of harmful compounds (Zackrisson et al., 1996; Wardle et al., 1998). Lower survivorship of *Picea mariana* and *Pinus banksiana* seedlings on more severely burned sites has been attributed to the formation of a hydrophobic crust on top of mineral soil (Sirois, 1993). Burning of deep organic deposits can leave substantial ash, and ash inhibits seedling emergence in *Pinus banksiana* (Thomas and Wein, 1990; Thomas and Wein, 1994; Herr and Duchesne, 1995). Mosses can inhibit seedling growth because of the large variability in temperature and moisture, the low nutrient supply, and possibly because of allelopathic compounds released in the forest floor (e.g., Fisher, 1979). Although the forest floor may generally be inimical to seedling establishment, rotten logs tend to provide good microsites for conifer seedlings (Timoney and Wein, 1991; DeLong et al., 1997; Hornberg et al., 1997; Simard et al., 1998) and the forest floor can provide a better seed bed than mineral soil for vascular plants competing with mosses (Jonsson and Esseen, 1998). Although much has to be learnt about the mechanisms, the amount and character of the forest floor is undoubtedly an important control on regeneration.

Succession

In the longer term, the forest floor exerts strong controls on succession. The most detailed studies have been carried in interior Alaska and summarized by van Cleve et al. (1991). In early stages of succession the main role of the forest floor is nutrient accumulation. As hardwoods dominate, the forest floor promotes succession to *Picea glauca* because hardwood seeds cannot regenerate on forest floors. Replacement of hardwood litter by spruce litter provides an inhospitable medium for vascular plant establishment and growth. Mosses flourish, leading to cooler soils and also further reducing litter quality, i.e., the ease with which litter can be decomposed. This slows forest floor decomposition rates giving deeper forest floors which cause further soil cooling and permafrost in many areas. *Picea glauca* eventually gives way to *Picea mariana*, the final successional stage. These successional processes have been successfully tested in a model that simulates tree establishment, growth, competition and mortality, soil microclimate and forest floor development (Bonan, 1990a; Bonan, 1990b). It should be noted that a recent study casts doubts on the mechanisms of the final successional stage, at least in floodplains (Mann et al., 1995).

Atmospheric interactions

Recently, considerable research has focussed on forest-atmosphere interactions, particularly the fluxes of carbon, heat and moisture. The forest floor is a major source of carbon efflux from respiration (e.g., Baldochi and Vogel, 1996; Lindroth et al., 1998; Russell and Voroney, 1998) and can account for more respiration than the mineral soil horizons combined (Figure 2 Pietikainen et al., 1999). It can also be a significant sink for the important greenhouse gas, methane (Amaral and Knowles, 1997; Savage et al., 1997). It can also be important for heat and moisture exchanges. For instance, 20-30% of the mass and energy exchange in a mature *Pinus banksiana* stand occurs at the forest floor (Baldochi and Vogel, 1996). The influence of forest floor characteristics on these fluxes cannot be ignored.

Faunal habitat

It must also be remembered that the forest floor is the habitat for many faunal species, some of which may affect tree growth and survival. In terms of carbon pools, they represent a very small proportion of the forest floor (Figure 5 Eijsackers and Zehnder, 1990), but may have impacts nevertheless. Densities of soil fauna can reach 1792 m^{-2} for microathropods (Paquin and Coderre, 1997) and 1607 m^{-2} for gastropods (Hawkins et al., 1997). Ants are active in most areas and may have an important role in consuming and redistributing seeds; ant mounds can provide habitat for earthworms (Laakso and Setala, 1997) which are important in their own right for litter breakdown. Slug predation of seedlings can be a problem and has been found to vary with forest floor moisture in *Pinus sylvestris* (Nystrand and Granstrom, 1997). The effect of the forest floor on trees via resident fauna is little studied, but cannot be dismissed as inconsequential.

Impacts of climate change

Of interest here is whether the forest floor is likely to be a source or sink of carbon in the coming decades. Will climate change alter forest floor carbon storage, and if so, by how much?

Forest floor carbon storage may be affected by a number of factors which are sensitive to climate: (1) forest productivity (2) decomposition rates, (3) forest composition, and (4) disturbance intervals.

Productivity

Climate can alter productivity, and hence litter input to the forest floor. Productivity generally increases with increasing temperature, a trend apparent across biomes (Figure 13 van Cleve et al., 1983a) and within the boreal (Kauppi and Posch, 1985; van Cleve et al., 1986; Beuker et al., 1996; Kauppi et al., 1997; Briffa et al., 1998). GCM predictions indicate large temperature increases in boreal regions for a double-CO_2 scenario (Figure 2 Flannigan et al., 1998) which suggests a substantial increase in productivity. Responses to precipitation changes are less clear, partially due the interactive effect of temperature on soil moisture. However, simulations combining effects of projected changes in temperature and precipitation show general increases in productivity (Pastor and Post, 1988; Karjalainen, 1996; Sykes and Prentice, 1996a) with further increases when the fertilisation effects of elevated CO_2 (Long et al., 1996) are taken into account (Melillo et al., 1993; Kellomäki and Väisänen, 1997). Increased nitrogen deposition may also increase productivity (Chen et al., 2000). Set against such productivity increases, however, is the possibility of enhanced decomposition.

Decomposition rates

Increased litterfall may be offset by changes in decomposition rates, which can occur due to changes in climate and litter quality. Climate clearly influences decomposition rates: litter decay can be related to mean annual temperature (Moore et al., 1999), actual evapotranspiration (AET) (Meentemeyer, 1978), an index of soil temperature and moisture (Berg et al., 1990), degree days and precipitation (Johansson, 1994; Kurka and Starr, 1997), forest floor heat sum (Fox and van Cleve, 1983) and litter moisture (Virzo De Santo et al., 1993). In general, decomposition rates increase with higher temperature and moisture regimes. The elevated temperatures predicted by GCM's should increase decomposition. There is no clear trend in GCM predictions for soil moisture (Figure 5.8 Mitchell et al., 1990), so the effects of these changes are uncertain. At the same time, increasing CO_2 concentrations will affect litter quality.

Many studies of boreal litters have related decomposition rates to litter quality (Meentemeyer, 1978; Berg et al., 1982; Flanagan and van Cleve, 1983; Fox and van Cleve, 1983; Berg and Ågren, 1984; Berg et al., 1984; Meentemeyer and Berg, 1986; Aber et al., 1990; Berg et al., 1990; Taylor et al., 1991; Huang and Schoenau, 1997a; Moore et al., 1999). Litter quality is often quantified in terms of ratios involving nitrogen and lignin content. In general, high lignin contents retard decomposition rates while high nitrogen contents promote decay, although some studies suggest that nitrogen content has no effect (Fyles and McGill., 1987; Alban and Pastor, 1993; Johansson, 1994; Prescott, 1995; Prescott et al., 1995) and there is evidence that high nitrogen concentrations are rate-retarding in late stages of decay (Berg, 2000). Plants grown in elevated CO_2 generally have lower nitrogen contents; changes in lignin contents also occur, but are usually small and may be positive or negative (Table 9.1 Melillo, 1996; Table 5 Moore et al., 1999). As atmospheric CO_2 concentrations rise, litter quality and therefore decay rates can be expected to change (see review in O'Neill and Norby, 1996), possibly decreasing decay rates. It remains an open question, however, whether this effect will be significant in relation to temperature-mediated increases and what will be the overall balance between decomposition and litter inputs.

Forest composition

The distribution of species on the boreal landscape is also sensitive to climate (Bradshaw and Zackrisson, 1990; Desponts and Payette, 1993; Landhäusser and Wein, 1993; Hogg and Schwarz, 1997). Most simulations predict dramatic changes under climate change scenarios (Pastor and Post, 1988; Campbell and McAndrews, 1993; Burton and Cumming, 1995; Sykes and Prentice, 1995; Price and Apps, 1996; Sykes and Prentice, 1996b; Chapin III and Starfield, 1997; Thompson et al., 1998). There are few studies on the effect of species on forest floor carbon, but it seems clear from Table 1-1 that there can be substantial differences among species, e.g., *Picea* species have more forest floor carbon than *Pinus*. With such differences, replacement of one species by another can alter forest floor storage. For example, severe fires in northern Alberta can cause a switch from *Picea mariana* stands with deep organic deposits to *Pinus banksiana* dominated stands with thin forest floors (R.W. Wein, pers. comm.). Such changes will depend on disturbance regimes and the availability of propagules (Overpeck et al., 1990; Weber and Flannigan, 1997). Over time, they may cause substantial change in forest floor carbon storage.

As an example, consider Canada, which has about a quarter of the world's boreal forest (Table 1 Apps et al., 1993). Potential changes in forest floor carbon storage have been calculated by multiplying the average forest floor C density of eight boreal tree species by the simulated changes in area of these species for two double-CO_2 equilibrium climates. The climate predictions come from the Goddard Institute for Space Studies (GISS) (Hansen et al., 1988) and the Geophysical Fluid Dynamics Laboratory (GFDL) (Manabe and Wetherald, 1987). Mean forest floor carbon densities for each species were calculated from data in Siltanen et al. (1997) and changes in area were taken from Figure 6 of Lenihan and Neilson (1995). Forest floor carbon increased by 1.2 GtC for the GFDL climate and decreased by 9.0 GtC for the GISS climate. The wide discrepancy reflects the many uncertainties in GCM predictions, but the point here is the potential for large changes in forest floor carbon storage, and by implication, fluxes to the atmosphere. To put these numbers in perspective, the double CO_2 scenarios imply a concomitant increase in atmospheric carbon of about 750 GtC.

Disturbance intervals

The forest floor carbon pool is also sensitive to disturbance intervals. The balance between litter input and decomposition is periodically interrupted by disturbances, which may remove all or part of the forest floor. In boreal forests, fire is the major agent of disturbance and stand-replacing fires dominate. In such fires, most of the forest floor is consumed by the flaming front during the fire and by smouldering combustion after the fire, and the remainder is likely to decline in the subsequent decade due to reduced litter input and more favourable conditions for decomposition. Fire regimes have historically been sensitive to climate (Clark, 1988; Bradshaw and Zackrisson, 1990; Clark, 1990; Bergeron and Flannigan, 1995; Larsen, 1997) and are expected to change considerably under climate change scenarios (Kurz et al., 1995; Weber and Flannigan, 1997; Flannigan et al., 1998).

To assess the potential for change, the effect of differing fire cycles was simulated. Given the lack of data on forest floor dynamics, the simple logarithmic function shown in Figure

1-4a was used. This assumes partial removal of forest floor by fire and no effect of species or climate. For an area equal to the global boreal forest (excluding peatlands) (Apps et al., 1993), the area in each age class (by year) was calculated assuming a constant risk of fire with age, i.e., a negative exponential model (Johnson, 1992), and this was multiplied by the forest floor C density for this age. The totals were summed for all age classes up to 1000 years to obtain the total forest floor carbon pool, and this was repeated for a range of fire cycles. The results (Figure 1-4b) show that total storage is sensitive to fire cycle. For example, a reduction from 100 years, which is typical of boreal forests (Johnson, 1992; Payette, 1992; Flannigan et al., 1998), to say 75 years, reduces total storage by 2.2 GtC. This is not in any sense meant to be a prediction, merely to indicate the potential for change. Even when averaged over the time scales of climate change, these changes may be significant.

Of course fire is not the only disturbance. In Canada, for example, insects have historically affected comparable areas (Figure 3 Kurz and Apps, 1999). Insect attack does not remove the forest floor in the same dramatic way as fire, but alters the input/output balance and predisposes the stand to increased risk of fire. However, it is far from clear the extent to which a changing climate will alter insect disturbance regimes (Fleming and Volney, 1995; Volney and Fleming, 2000). Harvesting also affects large areas of the boreal forest (e.g., Figure 3 Kurz and Apps, 1999) but disturbance intervals are controlled by human management rather than climate. Nevertheless, the impacts on the forest floor carbon storage cannot be ignored. Harvest operations can mix forest floor materials with mineral soil, and as with fire, decomposition is likely to increase while annual litter inputs decrease for several years after harvest. Consequently, the forest floor may decrease substantially in the years after harvest. Conversely, if there is no site preparation, which is common after harvest of *Populus tremuloides*, then most of the forest floor may remain leading to thicker forest floors during the second rotation.

Resolving uncertainties

There is clearly the potential for significant changes in forest floor carbon pools as a result of climate change, but as yet it is not possible to assess the magnitude or even the sign of such changes. To begin to resolve these uncertainties, forest floor dynamics need to be characterized over the life of stands for a range of factors. As discussed earlier, climate is likely to be an important factor influencing forest floor development. Tree species can also be expected to be an important factor because of differences in quantity and quality of litter.

Experimental data, however, are difficult to acquire due to the long life of forest stands, typically decades to centuries. Repeated observation is impracticable over the time horizon of most researchers. Tree growth is commonly measured from tree ring data, but unfortunately, there is no analogue for the forest floor. Dynamics can be inferred from measurements of inputs and outputs for a range of ages, but these inputs and outputs are large relative to annual increments and existing techniques do not allow for accurate measurement of either. Dynamics have been inferred from ^{14}C analyses (Trumbore and Harden, 1997), but are subject to many assumptions including that of first-order decay which may be inappropriate for the timescales of interest (Parton et al., 1987; Berg et al., 1995). One approach that offers promise is the use of chronosequences, whereby stands of different ages growing under the same or similar conditions are sampled and dynamics inferred from the time series of data. This technique is commonly used for long-term studies (e.g., Stoeckeler, 1961; Auclair, 1985; Bormann and Sidle, 1990; Bergeron and Dansereau, 1993; De Grandpré et al., 1993; Paré and Bergeron, 1995; Clark et al., 1998; Driscoll et al., 1999; Schulze et al., 1999). Though subject to many problems (Pickett, 1989; Yanai et al., 2000), it is believed that chronosequences are a viable technique for characterizing patterns and the approximate magnitude of forest floor development as well as assessing the effects of major factors such as species and climate.

Nevertheless, chronosequence data can only provide limited guidance on the impacts of climate change. First, there are many variables other than climate and species, such as soil texture, that may affect forest floor development. Identifying and sampling suitable stands for chronosequences is time-consuming and expensive; therefore chronosequences can only be realistically developed for a limited range of conditions. Second, chronosequences reveal patterns determined by past conditions, but conditions can be expected to be quite different in the future. Increased CO_2, higher levels of N deposition and greater climate variability are just some of the expected changes (Melillo et al., 1996; Nicholls et al., 1996) that would weaken extrapolations from past data. Consequently, predictions of future impacts will have to rely on computer models that are capable of simulating the effects of changed conditions expected under climate change scenarios.

Many models have examined climate change impacts on boreal forests, but few explicitly represent the forest floor and its affects on soil microclimate, nutrient cycling, rooting habitat and regeneration. Of those that do (e.g., Post and Pastor, 1996; Kellomäki and Väisänen, 1997; Grant and Nalder, 2000), none has been validated for forest floor dynamics under boreal conditions. This is not surprising, given the current lack of observed data. Data from the proposed chronosequence studies can be expected to be valuable in assessing the ability of current models to simulate forest floor dynamics, and providing validation data for new models if necessary.

Conclusion

The forest floor in boreal forests represents a substantial store of carbon which is likely to be sensitive to climate. It may, therefore, form a significant source or sink of atmospheric carbon under a changing climate. It also exerts important controls on the development of trees and other vegetation. It is important, therefore, to understand how the forest floor develops over time. Unfortunately, few data exist for these dynamics in boreal forests. It is believed that chronosequence studies offer the most promise for elucidating these dynamics and testing the effects of different factors. Data from such studies can be used to test or develop suitable computer models with a view to quantifying potential forest floor feedbacks on climate change.

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Tables

Table 1-1. Summary of boreal forest C density values (kgC m^{-2}) reported in the literature. Unless otherwise noted, tree and root refers to aboveground and belowground tree carbon respectively, soil refers to mineral soil carbon to a depth of 1 m, and carbon in coarse woody debris, understory and peat are not included. Where applicable oven-dry biomass data have been converted to carbon assuming 50% C content.

Location	Tree	Root	L	F	H	Soil	Note
Global/regional measures							
Global boreal forests	10.8		1.8	15.0			1
Global boreal forest biome	5.1		18.5				2
North American boreal forest	1.9						3
Canadian boreal ecoclimatic provinces	2.2						4
Canadian boreal ecoclimatic provinces			3.2			6.2	5
Western Canadian upland boreal forest	8.3		2.9			8.0	6
Finland, upland forests	4.3			7.2			7
Finland, mature upland coniferous sites	10.0			1.94		5.36	8
Former Soviet Union Taiga	6.1	2.0	1.3	28.1			9
Russia, Taiga stocked forests	3.75						10
Site-specific measures							
Interior Alaska, mature *Picea mariana*	2.5		3.8				11
Interior Alaska, mature *Picea glauca*	8.7		3.7				11
Interior Alaska, mature quaking *Populus tremuloides*	5.5		2.4				11
Interior Alaska, mature *Betula papyrifera*	5.6		2.9				11
Interior Alaska, mature *Populus balsamea*	6.0		1.1				11
Quebec, Canada, *Picea mariana*-lichen woodland	1.4		1.8				12
Quebec, Canada, *Picea mariana* chronosequence	0.5		0.1	0.0	1.8	10.2	13
New Brunswick, Canada, *Pinus banksiana* chrono.	2.2		5.1				14
Ontario, Canada. *Pinus banksiana*			1.8				15
Ontario, Canada, mature *Picea mariana*	6.9	2.0	7.0			9.0	16
Ontario, Canada, mature *Pinus banksiana*	6.2	1.0	2.0			4.9	16
U.S.A. Lake States, *Pinus banksiana* forest type	4.6		1.5			6.9	17
U.S.A. Lake States, *Abies balsamea* forest type	6.4		2.2			15.8	17
U.S.A. Lake States, *Populus tremuloides* forest type	6.5		1.3			12.4	17
Ontario, Canada, mature *Pinus banksiana*	8.2		2.1			4.9	18
Quebec, Canada, successional sequence			0.4	1.21			19
Russia, *Pinus sylvestris* forests			1.1				20
Canada, BOREAS SSA, young *Pinus banksiana* site	1.2		1.8			2.0	21
Canada, BOREAS SSA, old *Pinus banksiana* site	3.1		1.5			1.4	21
Canada, BOREAS SSA, *Populus tremuloides* site	9.3		1.9			3.6	21
Canada, BOREAS NSA, young *Pinus banksiana* site	0.8		4.0			2.8	21
Canada, BOREAS NSA, old *Pinus banksiana* site	2.3		1.1			2.6	21
Canada, BOREAS NSA, *Populus tremuloides* site	5.6		1.6			9.7	21
Canada, BOREAS NSA, mature *Pinus banksiana*	3.5	0.6	0.8			4.4	22
Canada, BOREAS SSA, mature *Pinus banksiana*	4.8	0.9	0.5			2.3	22
Canada, BOREAS SSA, mature *Populus tremuloides*			4.7			5.2	23
U.S.A. Lakes States, *Populus tremuloides*	8.9		6.4				24
U.S.A. Minnesota, mature stands on loam soil	8.5	1.9	1.5			4.1	25
U.S.A. Minnesota, mature stands on sand soil	7.4	1.2	1.2			4.1	25

[1] Atjay et al. (1979). This value is now recognized to be an overestimate because of biased sampling.

[2] Apps et al. (1993). Includes peatland areas.

[3] Botkin and Simpson (1990). Includes shrubs.
[4] From data in Kurz et al. (1992). Based on forested land, including peatland areas.
[5] From data in Siltanen et al. (1997). Mean of 660 sites.
[6] From data in Halliwell et al. (1997a) and Halliwell et al. (1997b). Means of 73 upland stands on N-S transect.
[7] Kauppi et al. (1997). Mineral soil to 75 cm.
[8] From data in Liski and Westman (1995). Means of 30 sites in southern Finland.
[9] Kolchugina and Vinson (1993). Values include peatlands and peat.
[10] Alexeyev et al. (1995). Includes peatland areas.
[11] van Cleve et al. (1983b).
[12] Auclair and Rencz (1982). Assuming forest floor is 80% organic matter.
[13] From data in Auclair (1985). Mean of 10 stand post-fire chronosequence. Soil to 40cm or bedrock
[14] From data in MacLean and Wein (1978). Means of 4 stand chronosequence.
[15] Weber (1987). Mean of 5 stands.
[16] Morrison et al. (1993).
[17] Approximate values from data in Grigal and Ohmann (1992).
[18] Mean of two stands from data in Foster et al. (1995). Soil to depth of 60 cm.
[19] From data in Paré et al. (1993).
[20] Mean of 18 forest sites across Russia from data in Gorshkov et al. (1996)
[21] Gower et al. (1997). Mineral soil to 70 cm. Tree includes understory.
[22] From data in Vogel and Gower (1998). Means of 2 stands. Fine roots excluded.
[23] Huang and Schoenau (1996). Mean of data from 5 slope positions.
[24] From data in Alban and Perala (1992). Means of 8 sites of varying ages. Soil to 50 cm.
[25] Means of four species from data in Perala and Alban (1982). Soil to 61 cm.

Figures

Figure 1-1. Amount of research categorized by forest structural layer based on abstracts cited in Current Contents™ during 1997 and 1998 containing the words "boreal" and "forest".

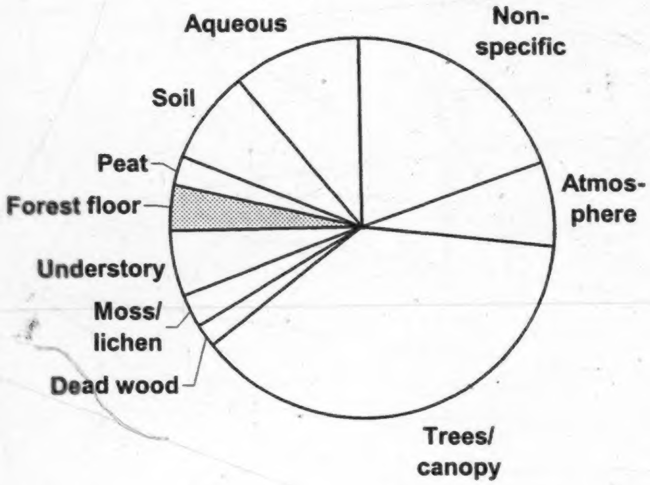


Figure 1-2. Variation of bulk density by forest floor layer and mineral soil horizon for *Populus tremuloides* site in Saskatchewan, Canada (data summarized from Huang and Schoenau, 1996).

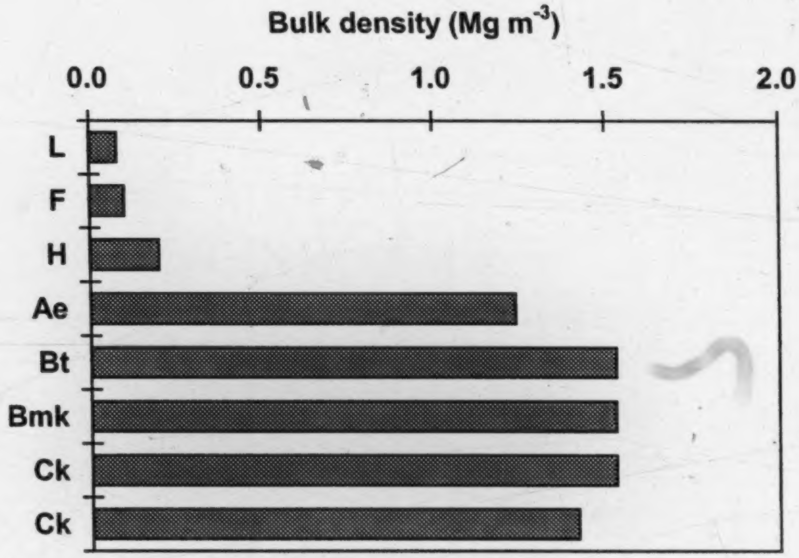


Figure 1-3. Variation of C:N ratio (g g^{-1}) by forest floor layer and mineral soil horizon for sites on loam soil in Minnesota (data summarized from Alban, 1982).

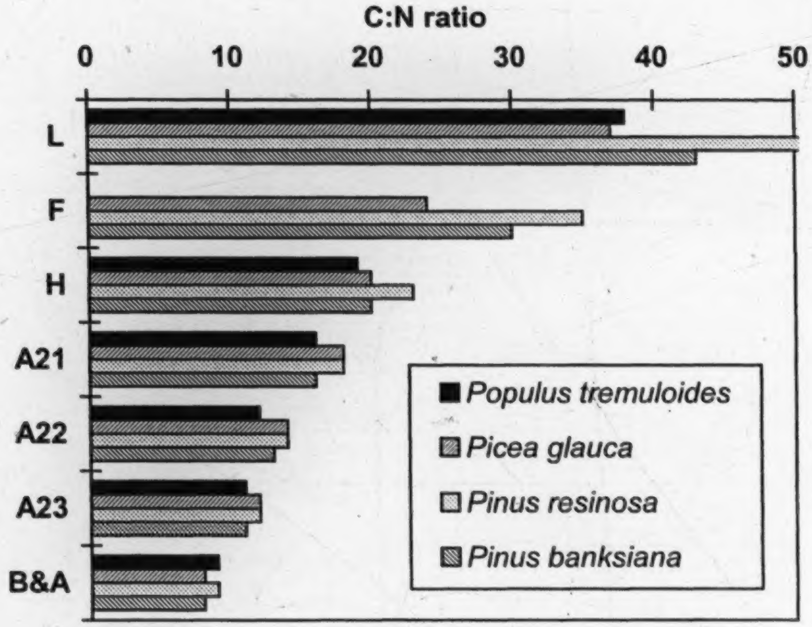
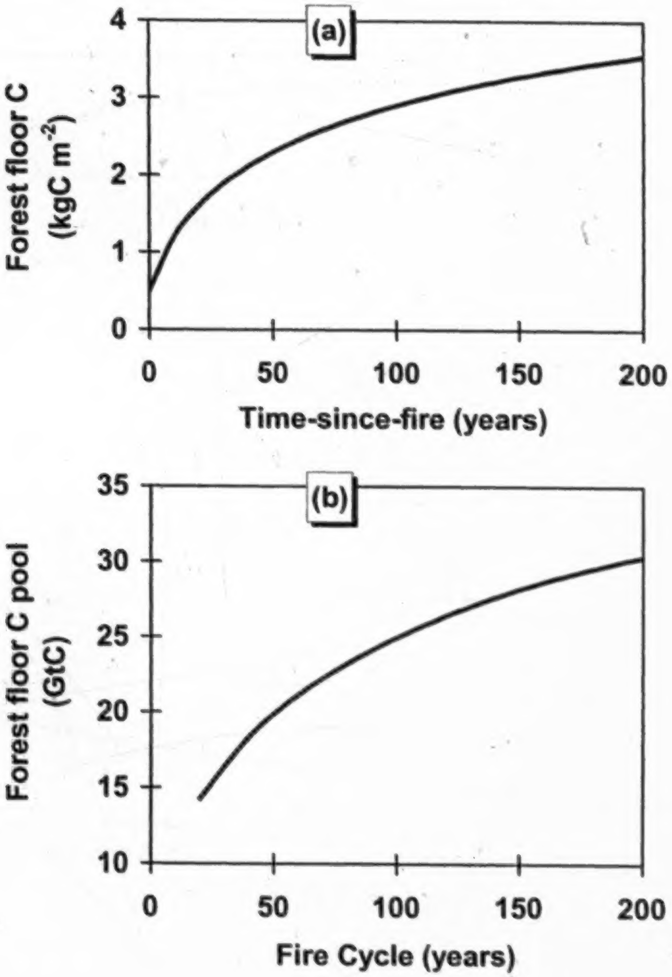


Figure 1-4. Sensitivity of forest floor carbon storage to fire cycle (a) assumed relationship between forest floor C density and time since disturbance, (b) forest floor carbon storage for an area equal to that of upland boreal forests for a range of fire cycles. See text for method of calculation.



References

Aber, J.D., Melillo, J.M. and McClaugherty, C.A., 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Can. J. Bot., 68: 2201-2208.

Agriculture Canada Expert Committee on Soil Survey, 1987. The Canadian System of Soil Classification. Publ. 1646. Agric. Can., Ottawa, Ontario, Canada.

Alban, D.H., 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. Soil Sci. Soc. Am. J., 46: 853-861.

Alban, D.H. and Pastor, J., 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res., 23: 1744-1749.

Alban, D.H. and Perala, D.A., 1992. Carbon storage in Lake States aspen ecosystems. Can. J. For. Res., 22: 1107-1110.

Alexeyev, V., Birdsey, R., Stakanov, V. and Korotkov, I., 1995. Carbon in vegetation of Russian forests: methods to estimate storage and geographic distributions. Water, Air, Soil Pollut., 82: 271-282.

Amaral, J.A. and Knowles, R., 1997. Localization of methane consumption and nitrification activities in some boreal forest soils and the stability of methane consumption on storage and disturbance. J. Geophy. Res., 102(D24): 29255-29260.

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G. and Vinson, T.S., 1993. Boreal forests and tundra. Water, Air, Soil Pollut., 70: 39-53.

Atjay, G.L., Ketner, P. and Duvigneaud, P., 1979. Terrestrial Primary Production and Phytomass. In: B. Bolin, E. Degens, S. Kempe and P. Ketner (Eds.). The Global carbon cycle. Workshop on the Carbon Cycle, 1977, Ratzeburg, Germany, Chichester, West Sussex, Scope No.13, pp. 129-182.

Auclair, A.N.D., 1985. Post-fire regeneration of plant and soil organic pools in a *Picea mariana-Cladonia alpestris* ecosystem. Can. J. For. Res., 15: 279-291.

Auclair, A.N.D. and Rencz, A.N., 1982. Concentration, mass and distribution of nutrients in a subarctic *Picea mariana-Cladonia alpestris* ecosystem. Can. J. For. Res., 12: 947-968.

Baldochi, D.D. and Vogel, C., 1996. Energy and CO_2 flux densities above and below a temperate broadleaved forest and a boreal pine forest. Tree Physiol., 16: 5-16.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Man., 133: 13-22.

Berg, B. and Ågren, G.I., 1984. Decomposition of needle litter and its organic chemical components: theory and field experiments. Long-term decomposition in a Scots pine forest. Can. J. Bot., 62: 2880-2888.

Berg, B., Ekbohm, G. and McClaugherty, C., 1984. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long term decomposition in a Scots pine forest IV. Can. J. Bot., 62: 2540-2550.

Berg, B., Jansson, P.-E. and McClaugherty, C., 1990. Climate variability and litter decomposition, results from a transect study. In: Boer, M. and deGroot, R.S., (Editors). Landscape Ecological Impact of Climatic Change. IOS Press, Amsterdam, pp. 250-269.

Berg, B., McClaugherty, C., Virzo De Santo, A., Johansson, M.-B. and Ekbohm, G., 1995. Decomposition of litter and soil organic matter: can we distinguish a mechanism for soil organic matter buildup? Scand. J. For. Res., 10: 108-119.

Berg, B., Wessen, B. and Ekbohm, G., 1982. Nitrogen level and decomposition in Scots pine needle litter. Oikos, 38: 291-296.

Bergeron, Y. and Dansereau, P.-R., 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. J. Veg. Sci., 4: 827-832.

Bergeron, Y. and Flannigan, M.D., 1995. Predicting the effects of climate change on fire frequency in the southeastern Canadian boreal forest. Water, Air, Soil Pollut., 82: 437-444.

Beuker, E., Kolstrom, M. and Kellomaki, S., 1996. Changes in wood production of *Picea abies* and *Pinus sylvestris* under a warmer climate: comparison of field measurements and results of a mathematical model. Silva Fennica, 30(2-3): 239-246.

Bonan, G.B., 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecol. Model., 45: 275-306.

Bonan, G.B., 1990a. Carbon and nitrogen cycling in North American boreal forests I. Litter quality and soil thermal effects in interior Alaska. Biogeochem., 10: 1-28.

Bonan, G.B., 1990b. Carbon and nitrogen cycling in North American boreal forests II. Biogeographic patterns. Can. J. For. Res., 20: 1077-1088.

Bonan, G.B., 1992. Soil temperature as an ecological factor in boreal forests. In: Shugart, H.H., Leemans, R. and Bonan, G.B., (Editors). A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, UK, pp. 126-144.

Bormann, B.T. and Sidle, R.C., 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. J. Ecology, 78: 561-578.

Botkin, D.B. and Simpson, L.G., 1990. Biomass of the north American boreal forest, a step toward accurate global measures. Biogeochem., 9: 161-174.

Bradshaw, R.H.W. and Zackrisson, O., 1990. A two thousand year history of a northern Swedish boreal forest stand. J. Veg. Sci., 1: 519-528.

Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G. and Vaganov, E.A., 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature, 391(6668): 678-682.

Burton, P.J. and Cumming, S.G., 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water, Air, Soil Pollut., 82: 401-414.

Campbell, I.D. and McAndrews, J.H., 1993. Forest disequilibrium caused by rapid Little Ice Age cooling. Nature, 366: 336-339.

Carleton, T.J. and Read, D.J., 1991. Ectomycorrhizas and nutrient transfer in conifer-feathermoss ecosystems. Can. J. Bot., 69: 778-785.

Chapin III, F.S. and Starfield, A.M., 1997. Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. Clim. Change, 35(4): 449-461.

Chen, W.J., Chen, J.H. and Cilar, J., 2000. An integrated terrestrial ecosystem carbon-budget model based on changes in disturbance, climate, and atmospheric chemistry. Ecol. Model., 135(1): 55-79.

Clark, D.F., Kneeshaw, D.D., Burton, P.J. and Antos, J.A., 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Can. J. For. Res., 28(2): 284-290.

Clark, J.S., 1988. Effect of climate change on fire regimes in northwestern Minnesota. Nature, 334: 233-234.

Clark, J.S., 1990. Fire and climate change during the last 750 yr in northwestern Minnesota. Ecol. Monogr., 60(2): 135-159.

De Grandpré, L., Gagnon, D. and Bergeron, Y., 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci., 4: 803-810.

DeLong, H.B., Lieffers, V.J. and Blenis, P.V., 1997. Microsite effects on first year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res., 27: 1452-1457.

Desponts, M. and Payette, S., 1993. The Holocene dynamics of jack pine at its northern range limit in Québec. J. Ecology, 81: 719-727.

Driscoll, K.G., Arocena, J.M. and Massicotte, H.B., 1999. Post-fire soil nitrogen content and vegetation composition in Sub-Boreal spruce forests of British Columbia's central interior, Canada. For. Ecol. Man., 121(3): 227-237.

Eijsackers, H. and Zehnder, A.J.B., 1990. Litter decomposition: a Russian matriochka doll. Biogeochem., 11: 153-174.

Federer, C.A., 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. Can. J. For. Res., 14: 763-767.

Finer, L., Messier, C. and De Grandpre, L., 1997. Fine-root dynamics in mixed boreal conifer-broad-leafed forest stands at different successional stages after fire. Can. J. For. Res., 27(3): 304-314.

Fisher, R.F., 1979. Possible allelopathic effects of reindeer-moss (*Cladonia*) on jack pine and white spruce. For. Sci., 25: 256-260.

Flanagan, P.W. and van Cleve, K., 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can. J. For. Res., 13: 795-817.

Flannigan, M., Bergeron, Y., Engelmark, O. and Wotton, M., 1998. Future wildfire in circumboreal forests in relation to global warming. J. Veg. Sci., 9(1): 469-476.

Fleming, R.A. and Volney, W.J.A., 1995. Effects of climate change on insect defoliator population precesses in Canada's boreal forest: some plausible scenarios. Water, Air, Soil Pollut., 82: 445-454.

Forestry Canada Fire Danger Group, 1992. Development and structure of the Canadian Forest Fire Behaviour Prediction System. Inf. Rep. ST-X-3. Forestry Canada, Ottawa, Canada.

Foster, N.W., Morrison, I.K., Hazlett, P.W. and Hogan, G.D., 1995. Carbon and nitrogen cycling within mid- and late-rotation jack pine. In: McFee, W.W. and Kelly, J.M., (Editors). Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Inc., Madison, Wisconsin, USA, pp. 355-375.

Fox, J.F. and van Cleve, K., 1983. Relationships between cellulose decomposition, Jenny's k, forest-floor nitrogen, and soil temperature in Alaskan taiga forests. Can. J. For. Res., 13: 789-795.

Frandsen, W.H., 1997. Ignition probability in organic soils. Can. J. For. Res., 27: 1471-1477.

Fyles, J.W. and McGill., W.B., 1987. Decomposition of boreal forest litters from central Alberta under laboratory conditions. Can. J. For. Res., 17: 109-114.

Gordon, A.G., 1983. Nutrient cycling dynamics in differing spruce and mixedwood ecosystems in Ontario and the effects of nutrient removals through harvesting. In: Wein, R.W., Riewe, R.R. and Methven, I.R. (Editors). Resources and Dynamics of the Boreal Zone. Proceedings of a conference held at Thunder Bay, Ontario, August 1982, Thunder Bay, Ontario, Association of Canadian Universities for Northern Studies, pp. 97-118.

Gorham, E., 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Appl., 1(2): 182-195.

Gorshkov, V.V., Bakkal, I.J. and Stavrova, N.I., 1996. Postfire recovery of forest litter in Scots Pine forests in two different regions of Boreal Zone. Silva Fennica, 30(2-3): 209-219.

Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.M., Sutton, D.J., Bazzaz, A. and Munger, J.W., 1998. Sensitivity of boreal forest carbon balance to soil thaw. Science, 279(5348): 214-217.

Gower, S.T., Pongracic, S. and Landsberg, J.J., 1996. A global trend in belowground carbon allocation: Can we use the relationship at smaller scales? Ecology, 77(6): 1750-1755.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J. and Stow, T.K., 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophy. Res., 102(D24): 29029-29041.

Grant, R.F. and Nalder, I.A., 2000. Climate change effects on net carbon exchange of a boreal aspen-hazelnut forest: estimates from the ecosystem model *ecosys*. Global Change Biol., 6: 183-200.

Green, R.N., Trowbridge, R.L. and Klinka, K., 1993. Towards a taxonomic classification of humus forms. For. Sci. Monogr., 29: 1-48.

Grigal, D.F., McRoberts, R.E. and Ohmann, F.F., 1991. Spatial variation in chemical properties of forest floor and surface mineral soil in the north central United States. Soil Sci., 151: 282-290.

Grigal, D.F. and Ohmann, L.F., 1992. Carbon storage in upland forests of the Lake States. Soil Sci. Soc. Am. J., 56: 935-943.

Gundersen, P., Emmett, B.A., Kjonaas, O.J., Koopmans, C.J. and Tietema, A., 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. For. Ecol. Man., 101(1-3): 37-55.

Halliwell, D.H. and Apps, M.J., 1997a. BOReal Ecosystem-Atmosphere Study (BOREAS) biometry and auxiliary sites: overstory and understory data. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, Canada. 254 pp.

Halliwell, D.H. and Apps, M.J., 1997b. BOReal Ecosystem-Atmosphere Study (BOREAS) biometry and auxiliary sites: soils and detritus data. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, Canada. 235 pp.

Hansen, J., Fung, I., Lacis, A., Rind, D., Lebedeff, S., Ruedy, R. and Russell, G., 1988. Global climate changes as forecast by Goddard Institute for Space Studies three-dimensional model. J. Geophy. Res., 93D: 9341-9364.

Harden, J.W., O'Neill, K., Trumbore, S.E., Veldhuis, H. and Stocks, B.J., 1997. Moss and soil contributions to the annual net carbon flux in a maturing boreal forest. J. Geophy. Res., 102(D24): 28805-28816.

Harden, J.W., Sundquist, E.T., Stallard, R.F. and Mark, R.K., 1992. Dynamics of soil carbon during the deglaciation of the Laurentide Ice Sheet. Science, 258: 1921-1924.

Hawkins, J.W., Lankester, M.W., Lautenschlager, R.A. and Bell, F.W., 1997. Length-biomass and energy relationships of terrestrial gastropods in northern forest ecosystems. Can. J. Zoology, 75(3): 501-505.

Heinselman, M.L., 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res., 3: 329-382.

Herr, D.G. and Duchesne, L.C., 1995. Jack pine (*Pinus banksiana*) seedling emergence is affected by organic horizon removal, ashes, soil, water and shade. Water, Air, Soil Pollut., 82: 147-154.

Hogg, E.H. and Schwarz, A.G., 1997. Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. J. Biogeogr., 24: 527-534.

Hornberg, G., Ohlson, M. and Zackrisson, O., 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. Can. J. For. Res., 27(7): 1015-1023.

Huang, W.Z. and Schoenau, J.J., 1996. Forms, amounts and distribution of carbon, nitrogen, phosphorus and sulfur in a boreal aspen forest soil. Can. J. Soil Sci., 76: 373-385.

Huang, W.Z. and Schoenau, J.J., 1997a. Mass loss measurements and statistical models to predict decomposition of leaf litter in a boreal aspen forest. Commun. Soil Sci. Plant Anal., 28(11-12): 863-874.

Huang, W.Z. and Schoenau, J.J., 1997b. Seasonal and spatial variations in soil nitrogen and phosphorus supply rates in a boreal aspen forest. Can. J. Soil Sci., 77(4): 597-612.

IPCC, 2001. Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change [McCarthy, J.J., O.F. Canziani, N.A. Leary, D.J. Dokken, and K.S. White (Eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, 1032 pp.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. and Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia, 108(3): 389-411.

Johansson, M.-B., 1994. Decomposition rate of Scots pine needle litter related to site properties, litter quality, and climate. Can. J. For. Res., 24: 1771-1781.

Johnson, E.A., 1992. Fire and Vegetation Dynamics. Cambridge University Press, Cambridge, UK. 129 pp.

Jonsson, B.G. and Esseen, P.A., 1998. Plant colonisation in small forest-floor patches: importance of plant group and disturbance traits. Ecography, 21(5): 518-526.

Karjalainen, T., 1996. Model computations on sequestration of carbon in managed forests and wood products under changing climatic conditions in Finland. J. Env. Manage., 47(4): 311-328.

Kasischke, E.S., Christensen Jr., N.L. and Stocks, B.J., 1995. Fire, global warming, and the carbon balance of boreal forests. Ecol. Appl., 5: 437-451.

Kattenberg, A., Giorgi, G., Grassl, H., Meehl, G.A., Mitchell, J.F.B., Stougger, R.J., Tokioka, T., Weaver, A.J. and Wigley, T.M.L., 1996. Climate models - projections of future climate. In: Houghton, J.T., Meira Filho, J.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K., (Editors). Climate Change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, UK, pp. 283-357.

Kauppi, P. and Posch, M., 1985. Sensitivity of boreal forests to possible climatic warming. Clim. Change, 7: 44-54.

Kauppi, P.E., Posch, M., Hanninen, P., Henttonen, H.M., Ihalainen, A., Lappalainen, E., Starr, M. and Tamminen, P., 1997. Carbon reservoirs in peatlands and forests in the boreal regions of Finland. Silva Fennica, 31(1): 13-25.

Keane, R.E., Morgan, P. and Running, S.W., 1996. FIRE-BGC: A Mechanistic Ecological Process Model for Simulating Fire Succession on Coniferous Forest Landscapes of the Northern Rocky Mountains. Res. Pap. INT-RP-484. U.S.D.A. For. Serv., Intermountain Research Station, Ogden, Utah.

Kellomäki, S. and Väisänen, H., 1997. Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. Ecol. Model., 97: 121-140.

Kimmins, J.P., 1987. Forest Ecology. Macmillan Publishing Company, New York. 531 pp.

Klinka, K., Wang, Q. and Kayahara, G.J., 1994. Quantitative characterization of nutrient regimes in some boreal forest soils. Can. J. Soil Sci., 74: 29-38.

Kolchugina, T.P. and Vinson, T.S., 1993. Equilibrium analysis of carbon pools and fluxes of forest biomes in the former Soviet Union. Can. J. For. Res., 23: 81-88.

Krause, K., 1998. Forest floor mass and nutrients in two chronosequences of plantations: Jack pine vs. black spruce. Can J. Soil Sci., 78(1): 77-83.

Kurka, A.M. and Starr, M., 1997. Relationship between decomposition of cellulose in the soil and tree stand characteristics in natural boreal forests. Plant And Soil, 195(2): 273-281.

Kurz, W.A. and Apps, M.J., 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecol. Appl., 9(2): 526-547.

Kurz, W.A., Apps, M.J., Stocks, B.J. and Volney, W.J., 1995. Global climate change: disturbance regimes and biospheric feedbacks of temperate and boreal forests. In: Woodwell, G.M. and Mackenzie, F., (Editors). Biotic Feedbacks in the Global Climatic

System: Will the Warming Feed the Warming. Oxford University Press, Oxford, UK, pp. 119-133.

Kurz, W.A., Apps, M.J., Webb, T.M. and McNammee, P.J., 1992. The carbon budget of the Canadian Forest Sector: Phase I. Inf. Rep. NOR-X-326. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta, Canada.

Laakso, J. and Setala, H., 1997. Nest mounds of red wood ants (*Formica aquilonia*): hot spots for litter-dwelling earthworms. Oecologia, 111(4): 565-569.

Landhäusser, S.M. and Wein, R.W., 1993. Postfire vegetation recovery and tree establishment at the Arctic treeline: climate-change vegetation response hypotheses. J. Ecol., 81: 665-672.

Larsen, C.P.S., 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeogr., 24: 663-673.

Lenihan, J.M. and Neilson, R.P., 1995. Canadian vegetation sensitivity to projected climatic change at three organizational levels. Clim. Change, 30: 27-56.

Lindroth, A., Grelle, A. and Moren, A.S., 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. Global Change Biol., 4(4): 443-450.

Liski, J., 1995. Variation in soil organic carbon and thickness of soil horizons within a boreal forest stand - effect of trees and implications for sampling. Silva Fennica, 29(4): 255-266.

Liski, J., Ilvesniemi, H., Mäkelä, A. and Starr, M., 1998. Model analysis of the effects of soil age, fires and harvesting on the carbon storage of boreal forest soils. Eur. J. Soil Sci., 49(3): 407-416.

Liski, J. and Westman, C.J., 1995. Density of organic carbon in soil at coniferous forest sites in southern Finland. Biogeochem., 29: 183-197.

Liski, J. and Westman, C.J., 1997. Carbon storage in forest soil of Finland: 1. Effect of thermocline. Biogeochem., 36: 239-260.

Long, S.P., Osborne, C.P. and Humphries, S.W., 1996. Photosynthesis, rising atmospheric carbon dioxide concentration and climate change. In: Breymeyer, A.I., Hall, D.O., Melillio, J.M. and Agren, G.I., (Editors). Global Change: Effects on Coniferous Forests and Grasslands. John Wiley & Sons Ltd., New York, pp. 121-159.

MacLean, D.A. and Wein, R.W., 1977. Nutrient accumulation for postfire jack pine and hardwood succession patterns in New Brunswick. Can. J. For. Res., 7: 562-578.

MacLean, D.A. and Wein, R.W., 1978. Litter production and forest floor nutrient dynamics in pine and hardwood stands of New Brunswick, Canada. Holarctic Ecology, 1: 1-15.

Maini, J.S., 1967. Variation in vegetative propagation of *Populus* in natural populations. Bull. Ecol. Soc. Am., 48: 75-76.

Manabe, S. and Wetherald, R.T., 1987. Large-scale changes in soil wetness induced by an increase in carbon dioxide. J. Atm. Sci., 44: 1211-1235.

Mann, D.H., Fastie, C.L., Rowland, E.L. and Bigelow, N.H., 1995. Spruce succession, disturbance, and geomorphology on the Tanana River floodplain, Alaska. EcoSci., 2: 184-199.

Meentemeyer, V., 1978. Macroclimate and lignin control of litter decomposition rate. Ecology, 59: 465-472.

Meentemeyer, V. and Berg, B., 1986. Regional variation in mass-loss of *Pinus sylvestris* needle litter in Swedish pine forests as influenced by climate and litter quality. Scand. J. For. Res., 1: 167-180.

Melillo, J.M., 1996. Elevated carbon dioxide, litter quality and decomposition. In: Breymeyer, A.I., Hall, D.O., Melillo, J.M. and Agren, G.I., (Editors). Global Change: Effects on Coniferous Forests and Grasslands. John Wiley and Sons, New York, pp. 199-206.

Melillo, J.M., McGuire, A.D., Kicklighter, D.W., III, B.M., Vorosmarty, C.J. and Schloss, A.L., 1993. Global climate change and terrestrial net primary production. Nature, 363: 234-240.

Melillo, J.M., Prentice, I.C., Farquhar, G.D., Schulze, E.-D. and Sala, O.A., 1996. Terrestrial biotic responses to environmental change and feedbacks to climate. In: Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K., (Editors). Climate Change 1995: The Science of Climate Change. University of Cambridge, New York, NY, pp. 445-482.

Mitchell, J.F.B., Manabe, S., Meleshko, V. and Tokioka, T., 1990. Equilibrium climate change - and its implications for the future. In: Houghton, J.T., Jenkins, G.J. and Ephraums, J.J., (Editors). Climate Change: The IPCC Scientific Assessment. Cambridge University Press, Cambridge, pp. 131-172.

Moore, T.R., 1983. Winter time litter decomposition in a subarctic woodland. Arct. Alp. Res., 15: 413-418.

Moore, T.R., Trofymow, J.A., Taylor, B., Prescott, C., Camiré, C., Duschene, L., Fyles, J., Kozak, L., Kranabetter, M., Morrison, I., Siltanen, M., Smith, S., Titus, B., Visser, S., Wein, R. and Zoltai, S., 1999. Litter decomposition rate in Canadian forests. Global Change Biol., 5: 75-82.

Morrison, I.K., Foster, N.W. and Hazlett, P.W., 1993. Carbon reserves, carbon cycling, and harvesting effects in three mature forest types in Canada. N. Z. J. For. Sci., 23: 403-412.

Nalder, I.A. and Wein, R.W., 1998. A new forest floor corer for rapid sampling, minimal disturbance and adequate precision. Silva Fennica, 32(4): 373-382.

Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Högberg, M. and Högberg, P., 1998. Boreal forest plants take up organic nitrogen. Nature, 392: 914-197.

Nicholls, N., Gruza, G.V., Jouzel, J., Karl, T.R., Ogallo, L.A. and Parker, D.E., 1996. Observed climate variability and change. In: Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K., (Editors). Climate Change 1995: The Science of Climate Change. University of Cambridge, New York, NY, pp. 133-192.

Nystrand, O. and Granstrom, A., 1997. Forest floor moisture controls predator activity on juvenile seedlings of *Pinus sylvestris*. Can. J. For. Res., 27(11): 1746-1752.

Oke, T.R., 1987. Boundary layer climates. Second edition. Routledge, London, UK. 435 pp.

O'Neill, E.G. and Norby, R.J., 1996. Litter quality and decomposition rate of foliar litter produced under CO_2 enrichment. In: Kock, G.W. and Mooney, H.A., (Editors). Carbon Dioxide and Terrestrial Ecosystems. Academic Press, San Diego, pp. 87-103.

Overpeck, J.T., Rind, D. and Goldberg, R., 1990. Climate-induced changes in forest disturbance and vegetation. Nature, 343: 51-53.

Pajari, B., 1995. Soil respiration in a poor upland site of Scots pine stand subjected to elevated temperatures and atmospheric carbon concentration. Plant and Soil, 168-169: 563-570.

Paquin, P. and Coderre, D., 1997. Changes in soil macroarthropod communities in relation to forest maturation through three successional stages in the Canadian boreal forest. Oecologia, 112(1): 104-111.

Paré, D. and Bergeron, Y., 1995. Above ground biomass accumulation along a 230 year chronosequence in the southern portion of the Canadian boreal forest. J. Ecology, 83: 1001-1007.

Paré, D. and Bergeron, Y., 1996. Effect of colonization tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Can. J. For. Res., 26(6): 1022-1031.

Paré, D., Bergeron, Y. and Camiré, C., 1993. Changes in the forest floor of Canadian boreal forest after disturbance. J. Veg. Sci., 4: 811-818.

Parton, W.J., Schimel, D.S., Cole, C.V. and Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains Grasslands. Soil Sci. Soc. Am. J., 51: 1173-1179.

Pastor, J. and Post, W.M., 1988. Response of northern forests to CO_2-induced climatic change. Nature, 334: 55-58.

Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R. and Bonan, G.B., (Editors). A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, UK, pp. 145-169.

Perala, D.A. and Alban, D.H., 1982. Biomass, nutrient distribution and litterfall in *Populus*, *Pinus* and *Picea* stands on two different soils in Minnesota. Plant And Soil, 64: 177-192.

Persson, H., 1980. Death and replacement of fine roots in a mature Scots pine forest. In: Persson, T., (Editor). Structure and Function of Northern Coniferous Forests-An Ecosystem Study, Ecol Bull. 32, pp. 240-251.

Pickett, W.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E., (Editor). Long Term Studies in Ecology: Approaches and Alternatives. Springer-Verlag, New York, pp. 110-135.

Pietikainen, J., Vaijarvi, E., Ilvesniemi, H., Fritze, H. and Westman, C.J., 1999. Carbon storage of microbes and roots and the flux of CO_2 across a moisture gradient. Can. J. For. Res., 29(8): 1197-1203.

Post, W.M. and Pastor, J., 1996. Linkages - an individual-based forest ecosystem model. Clim. Change, 34(2): 253-261.

Prescott, C.E., 1995. Does nitrogen availability control rates of litter decomposition in forests? Plant and Soil, 168-169: 83-88.

Prescott, C.E., Kishchuk, B.E. and Weetman, G.F., 1995. Long-term effects of repeated N fertilization and straw application in a jack pine forest 3. Nitrogen availability in the forest floor. Can. J. For. Res., 25: 1991-1996.

Price, D.T. and Apps, M.J., 1996. Boreal forest responses to climate-change scenarios along an ecoclimatic transect in Central Canada. Clim. Change, 34(2): 179-190.

Pritchett, W.L. and Fisher, R.F., 1987. Properties and Management of Forest Soils. John Wiley & Sons Inc., New York. 494 pp.

Protz, R., Ross, G.J., Martini, I.P. and Terasmae, J., 1984. Rate of podzolic soil formation near Hudson Bay, Ontario. Can. J. Soil Sci., 64: 31-49.

Protz, R., Ross, G.J., Martini, I.P. and Terasmae, J., 1988. Podzolic soil development in the Southern James Bay lowlands, Ontario. Can. J. Soil Sci., 68: 287-305.

Raich, J.W. and Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology, 70(5): 1346-1354.

Ruark, G.A. and Bockheim, J.G., 1987. Below-ground biomass of 10-, 20-, and 32- year-old *Populus tremuloides* in Wisconsin. Pedobiologia, 30: 207-217.

Russell, C.A. and Voroney, R.P., 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. Can. J. Soil Sci., 78(2): 301-310.

Savage, K., Moore, T.R. and Crill, P.M., 1997. Methane and carbon dioxide exchanges between the atmosphere and northern boreal forest soils. J. Geophy. Res., 102(D24): 29279-29288.

Schimel, D., Alves, D., Enting, I., Heimann, M., Joos, F., Raynaud, D., Wigley, T., Prather, M., Derwent, R., Ehhalt, D., Fraser, P., Sanhueza, E., Shou, X., Jonas, P., Charlson, R., Rodhe, H., Sadasivan, S., Shine, K.P., Fouquart, Y., Ramaswamy, V., Solomon, S., Srinivasan, J., Albritton, D., Derwent, R., Isaksen, I., Lal, M. and Wuebbles, D., 1996. Radiative forcing of climate change. In: Houghton, J.T., Meira Filho, J.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K., (Editors). Climate Change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, UK, pp. 65-131.

Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biol., 1: 77-91.

Schlesinger, W.H., 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature, 348: 232-234.

Schulze, E.-D., Lloyd, J., Kelliher, F.M., Wirth, C., Rebmann, C., Luhker, B., Mund, M., Knohl, A., Milyukova, I.M., Schulze, W., Ziegler, W., Varlagin, A.B., Sogachev, A.F., Valentini, R., Dore, S., Grigoriev, S., Kolle, O., Panfyorov, M.I., Tchebakova, N. and Vygodskaya, N.N., 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink -- a synthesis. Global Change Biol., 5(6): 703-722.

Schulze, E.-D., Chapin III, F.S. and Gebauer, G., 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia, 100: 406-412.

Schulze, E.-D., Schulze, W., Kelliher, F.M., Vygodskaya, N.N., Ziegler, W., Kobak, K.I., Koch, H., Arneth, A., Kusnetsova, W.A., Sogatchev, A., Issajev, A., Bauer, G. and Hollinger, D.Y., 1995. Aboveground biomass and nitrogen nutrition in a chronosequence of pristine *Dahurian larix* stands in eastern Siberia. Can. J. For. Res., 25: 943-960.

Schwendenmann, L., 2000. Soil properties of boreal riparian plant communities in relation to natural succession and clear-cutting, Peace River lowlands, Wood Buffalo National Park, Canada. Water, Air, Soil Pollut., 122(3-4): 449-467.

Sharratt, B.S., 1997. Thermal conductivity and water retention of a black spruce forest floor. Soil Sci., 162(8): 576-582.

Siltanen, R.M., Apps, M.J., Zoltai, S.C., Mair, R.M. and Strong, W.L., 1997. A soil profile and organic carbon data base for Canadian forest and tundra mineral soils. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, Canada. 50 pp.

Simard, M.J., Bergeron, Y. and Sirois, L., 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci., 9(4): 575-582.

Sirois, L., 1993. Impact of fire on *Picea mariana* and *Pinus banksiana* seedlings in subarctic lichen woodlands. J. Veg. Sci., 4: 795-802.

Slaughter, K.W., Grigal, D.F. and Ohmann, L.F., 1998. Carbon storage in southern boreal forests following fire. Scand. J. For. Res., 13(2): 119-127.

Soil Survey Staff, 1981. Soil Survey Manual, Chapter 4. USDA Soil Conserv. Serv. Mimeo., Washington, D.C.

Stoeckeler, J.H., 1961. Organic layers in Minnesota aspen stands and their role in soil improvement. For. Sci., 7: 66-71.

Strong, W.L. and La Roi, G.H., 1983. Rooting depths and successional development of selected boreal forest communities. Can. J. For. Res., 13: 577-588.

Sykes, M.T. and Prentice, I.C., 1995. Boreal forest futures: modelling the controls on tree species range limits and transient responses to climate change. Water, Air, Soil Pollut., 82: 401-414.

Sykes, M.T. and Prentice, I.C., 1996a. Carbon storage and climate change in Swedish forests: a comparison of static and dynamic modelling approaches. In: Apps, M.J. and Price, D.T., (Editors). The Role of Forest Ecosystems, Forest Management and the Global Carbon Cycle. Proceedings of the NATO Advanced Research Workshop held at Banff, Canada, September 12-16, 1994. Springer, Berlin, pp. 69-78.

Sykes, M.T. and Prentice, I.C., 1996b. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. Clim. Change, 34(2): 161-177.

Taylor, B.R., Prescott, C.E., Parsons, W.J.F. and Parkinson, D., 1991. Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Can. J. Bot., 69: 2242-2250.

Thomas, P.A. and Wein, R.W., 1990. Jack pine establishment on ash from wood and organic soils. Can. J. For. Res., 15: 727-729.

Thomas, P.A. and Wein, R.W., 1994. Amelioration of wood ash toxicity and jack pine establishment. Can. J. For. Res., 24: 748-755.

Thompson, I.D., Flannigan, M.D., Wotton, B.M. and Suffling, R., 1998. The effects of climate change on landscape diversity: An example in Ontario forests. Environ. Monit. Assess., 49(2-3): 213-233.

Timoney, K.P. and Wein, R.W., 1991. The areal pattern of burned tree vegetation in the subarctic region of northwestern Canada. Arctic, 44: 223-230.

Trofymow, J.A. and CIDET Working Group, 1998. The Canadian Intersite Decomposition Experiment (CIDET): Project and Site Establishment Report. Inf. Rep. BC-X-378. Nat. Resour. Can., Can. For. Serv., Pac. For. Cent., Victoria, B.C.

Trumbore, S.E. and Harden, J.W., 1997. Input, accumulation, and turnover of carbon in soils of the BOREAS Northern Study Area. J. Geophy. Res., 102(D24): 28817-28830.

van Cleve, K., Barney, R. and Schlentner, R., 1981. Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. Can. J. For. Res., 11: 258-273.

van Cleve, K., Chapin III, F.S., Dyrness, C.T. and Viereck, L.A., 1991. Element cycling in taiga forests: State-factor control. BioSci., 41: 78-88.

van Cleve, K., Chapin III, F.S., Flanagan, P.W., Viereck, L.A. and Dryness, C.T. (Editors). 1986. Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function. Springer-Verlag, New York, NY, 230 pp.

van Cleve, K. and Noonan, L.L., 1975. Litterfall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. Can. J. For. Res., 5: 626-639.

van Cleve, K., Olivier, L., Schlentner, R., Viereck, L.A. and Dyrness, C.T., 1983a. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res., 13: 747-766.

van Cleve, K., Viereck, L.A. and Dyrness, C.T., 1983b. Dynamics of a black spruce ecosystem in comparison with other forest types: a multidisciplinary study in interior Alaska. In: Wein, R.W., Riewe, R.R. and Methven, I.R. (Editors). Resources and dynamics of the boreal zone, Thunder Bay, Ontario, Association of Canadian Universities for Northern Studies, pp. 148-166.

van Cleve, K. and Yarie, J., 1986. Interaction of temperature, moisture and soil chemistry in controlling nutrient cycling and ecosystem development in the Taiga of Alaska. In: van Cleve, K., Chapin III, F.S., Flanagan, P.W., Viereck, L.A. and Dyrness., C.T., (Editors). Forest Ecosystems in the Alaskan Taiga: a Synthesis of Structure and Function. Springer-Verlag, New York, pp. 160-189.

Van Wagner, C.E., 1983. Fire behaviour in northern conifer forests and shrublands. In: Wein, R.W. and McLean, D.A., (Editors). The Role of Fire in Northern Circumpolar Ecosystems. John Wiley & Sons, Chichester, UK, pp. 65-80.

Viereck, L.A., 1970. Soil temperatures in river bottom stands in interior Alaska. In: Ecology of the SubArctic Regions - Proceedings of the Helsinki Symposium, UNESCO, Paris, pp. 223-233.

Viereck, L.A. and Schandelmeier, L.A., 1980. Effects of Fire in Alaska and Adjacent Canada - a literature review. BLM Alaska Technical Report 6. Bureau of Land Management, U.S. Depart. Interior, Alaska.

Virzo De Santo, A., Berg, B., Rutigliano, F.A., Alfani, A. and Fioretto, A., 1993. Factors regulating early-stage decomposition of needle litters in five different coniferous forests. Soil Biol. Biochem., 25(10): 1423-1433.

Vogel, J.G. and Gower, S.T., 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. Ecosystems, 1(4): 386-400.

Volney, W.J.A. and Fleming, R.A., 2000. Climate change and impacts of boreal forest insects. Agriculture Ecosystem Environment, 82(1-3): 283-294.

Volokitina, A.V., 1996. Forest fuel maps. In: Goldammer, J.G. and Furyaev, V.V., (Editors). Fire in ecosystems of boreal Eurasia. Kluwer Academic Publishers, Dortrecht, pp. 239-252.

Wagener, S.M. and Schimel, J.P., 1998. Stratification of soil ecological processes: a study of the birch forest floor in the Alaskan taiga. Oikos, 81(1): 63-74.

Wardle, D.A., Zackrisson, O., Hörnberg, G. and Gallet, C., 1997. The influence of island area on ecosystem properties. Science, 277: 1296-1299.

Wardle, D.A., Zackrisson, O. and Nilsson, M.C., 1998. The charcoal effect in boreal forests: mechanisms and ecological consequences. Oecologia, 115(3): 419-426.

Weber, M.G., 1987. Decomposition, litter fall, and forest floor nutrient dynamics in relation to fire in eastern Ontario jack pine ecosystems. Can. J. For. Res., 17: 1496-1506.

Weber, M.G. and Flannigan, M.D., 1997. Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. Environ. Rev., 5: 145-166.

Wei, X. and Kimmins, J.P., 1998. Asymbiotic nitrogen fixation in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. For. Ecol. Man., 109(1-3): 343-353.

Wein, R.W., 1983. Fire behaviour and ecological effects in organic terrain. In: Wein, R.W. and McLean, D.A., (Editors). The Role of Fire in Northern Circumpolar Ecosystems. John Wiley & Sons, Chichester, UK, pp. 81-96.

Woodwell, G.M., Mackenzie, F.T., Houghton, R.A., Apps, M., Gorham, E. and Davidson, E., 1998. Biotic feedbacks in the warming of the earth. Clim. Change, 40(3-4): 495-518.

Yanai, R.D., Arthur, M.A., Siccama, T.G. and Federer, C.A., 2000. Challenges of measuring forest floor organic matter dynamics: repeated measures from a chronosequence. For. Ecol. Man., 138(1-3): 273-283.

Yin, X. and Arp, P., 1993. Predicting forest soil temperatures from monthly air temperature and precipitation records. Can. J. For. Res., 23: 2521-2536.

Zackrisson, O., Nilsson, M.-C. and Wardle, D.A., 1996. Key ecological function of charcoal from wildfire in the boreal forest. Oikos, 77: 10-19.

Zasada, J., 1986. Natural regeneration of trees and tall shrubs on forest sites in interior Alaska. In: van Cleve, K., Chapin III, F.S., Flanagan, P.W., Viereck, L.A. and Dyrness, C.T., (Editors). Forest Ecosystems in the Alaskan Taiga: a Synthesis of Structure and Function. Springer-Verlag, New York, pp. 44-73.

2. A new forest floor corer for rapid sampling, minimal disturbance and adequate precision[1]

Introduction

In upland boreal forests, there is little faunal mixing of decomposing litter with the underlying mineral soil, and consequently a distinctive organic layer soon develops. This comprises L, F and H layers (Agriculture Canada Expert Committee on Soil Survey, 1987), which may or may not be distinctly delineated. For many purposes it is convenient to treat the three layers as one and refer to them as the forest floor (Kimmins, 1987). The depth of the forest floor depends on many factors, including forest type, climate and stand history, and commonly ranges from 2 to 20 cm. The forest floor is important for nutrient cycling (van Cleve et al., 1983; Johnson, 1995), for forest fire fuel loads (Van Wagner, 1983, Forestry Canada Fire Danger Group, 1992), and for its role in regulating soil temperature and moisture (Bonan and Shugart, 1989). It is also important as a carbon pool, accounting for 28% of soil carbon storage in non-peatland forests of Finland (Liski and Westman, 1997) and up to one half of soil carbon in upland stands in western Canada (Huang and Schoenau, 1996). Yet it is difficult to characterize because spatial variability is high (Hokkanen et al., 1995; Liski, 1995). Consequently, a high number of samples is needed to achieve reasonably precise estimates for variables such as C density or bulk density.

The traditional method of forest floor sampling has been to extract a block, typically 30 by 30 cm square, by cutting around the perimeter of a template with a sharp knife, then lifting this block away from the mineral soil (e.g., van Cleve and Noonan, 1971; Alban, 1982; Quintilio et al., 1991; Paré and Bergeron, 1996; Gower et al., 1997). This is time consuming and gives large quantities of forest floor material to process; as a result, small sample numbers may not capture variability efficiently. Cylindrical push-corers of smaller cross sectional area are not uncommon (e.g., Westman, 1995; Zackrisson et al., 1995; Finer et al., 1997; Liski and Westman, 1997), but have two important limitations for forest floor sampling. First, they compress the layer and reduce its natural volume making it difficult to obtain reasonable bulk density measurements. Second, the fibric nature of forest floor materials can cause some material to be pushed away from the cutting edge, either inward or outward, which leads to overestimates or underestimates, respectively. This problem is particularly acute with small corers, where the ratio of perimeter to cross-sectional area is high. Push-corers also tend to deflect from particularly hard material, such as roots and pieces of dead wood, resulting in a crooked core and a biased estimate of forest floor mass. Ideally, a small diameter corer should make a clean, vertical cut through the forest floor with virtually no disturbance. Such a corer has been developed which is lightweight, inexpensive to fabricate, and allows cores to be taken much faster than traditional template methods. This corer has been used over three field seasons for sampling the forest floor, as well as the moss/lichen layer and shallow mineral soil, in stands dominated by *Picea glauca* (Moench) Voss (white spruce), *Populus tremuloides* Michx. (trembling aspen) and *Pinus banksiana* Lamb. (jack pine) in western Canada. Here the corer and its operation are described, data are presented on sampling variability and other applications are discussed.

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[1] A version of this chapter has been published. Nalder and Wein 1998. Silva Fennica. 32(4): 373-382.

Description and operation

Design and construction

The corer system consists of a sharpened length of steel water pipe driven by a battery-powered rotary drill through an adaptor unit (Figure 2-1). This system has become feasible with the recent wide availability of powerful drills driven by rechargeable batteries. Details of the corer and adaptor are shown in Figure 2-2. The tubular corer is made from standard, mild steel water pipe. Two-inch pipe (55.9 mm OD, 52.6 mm ID) was used, but the exact diameter is not critical; larger diameter pipe would require more torque, and battery life may be limiting. A pipe length of 30 cm was suitable for this study but it could be shorter or longer depending on the application. Two holes at the upper end take a quick-connect pin that couples the corer to the adaptor. The machined adaptor unit (Figure 2-2) comprises a 9.6 mm hexagonal shaft, which is clamped in the drill chuck, a cylinder whose outer diameter is such that it fits flush within the corer pipe, and a quick-connect pin that goes transversely though the cylinder. The motive force is provided by a standard, industrial-quality drill, which should have a 12 mm (½-inch) chuck. Because torque and battery life are critical, it is recommended that the drill have a torque rating of at least 34 N-m (300 inch-pounds), low-reduction gearing providing speeds of 350 rpm or less, and a battery of at least 12 volts. For most field applications, one or two spare rechargeable batteries will be required.

The last two components of the system are a light-weight core extractor and an examining tray (Figure 2-1b). The core extractor is a piece of ABS water pipe cut slightly longer than the corer and sealed at each end with plastic end caps. The pipe diameter should be chosen so that the end cap fits snugly into the steel corer pipe. In the North American system, a 4.4 cm (1¾-inch) ABS pipe works well with the two-inch corer. An examining tray is made from white polyvinyl chloride pipe of the same internal diameter and length as the corer. It is cut in half vertically, making one "half" slightly larger than the other. The longitudinal edges of the larger half are then flared out by heating and bending the plastic so that the soil core is securely held in the examining tray while the high sides prevent accidental loss of material. To aid in measuring layer depths, lines can be drawn around the inner circumference at 1-cm intervals.

A critical aspect of the system is a sharp corer. Sharpening can be done with the drill and a rotary sanding disc, which is how the edge is kept sharp in the field, but a belt sander (or grinder) is quicker and easier for the initial shaping of the edge. Sand first with coarse grit (#50) and work up to fine grit (#120). The angle of the edge should be 25-30 degrees and the edge must be scalloped. A peak-trough depth of 1-2 mm with a cycle interval (peak-peak distance) of 2 cm worked well. At this stage, it is also useful to scribe horizontal lines on the outside of the pipe to indicate the depth of coring (Figure 2-2).

Apart from the adaptor, which must be machined, the system can be put together by anyone with a modicum of mechanical skill. The system described here, including the drill, two rechargeable batteries, construction materials and machine shop charges, cost less than US$500.

Operation

To take soil cores, clamp the adaptor firmly in the drill chuck, clip the corer onto the adaptor, and hold the corer vertically over the sampling point (a 2-D level glued to the top of the drill can be helpful for keeping the corer vertical). Select the low-speed gear, engage the motor and slowly lower the corer, letting it cut through the moss and lichen layer (if present), through the L, F and H layers and into mineral soil. Only a slight weight is required on the cutting edge, therefore support the weight of the drill while coring; too much pressure may compress the sample, particularly moss, which will prevent proper bulk density measurements. Core a few centimetres into the mineral soil to create a base for the forest floor sample. Stop the drill and lift the corer out. Keeping the corer upright, disconnect it from the adaptor, put the top of the corer onto the base of the examining tray, insert the core extractor into the bottom of the corer and gently push the core out of the corer and onto the examining tray (Figure 2-1b). At this point, the layers can be identified, any extraneous material removed, depths of layers measured, and layers described as necessary. The required layers are then separated, usually with a sharp knife, and transferred to plastic bags for later laboratory analysis.

Practical aspects

Weighing only 3.5 kg, the complete corer system is easy to carry and can be operated by one person. It takes only a few seconds to drill a core and a few more seconds to extract it into the examining tray. The longest process is examination, separation of layers, description, and bagging of samples. Field time can be reduced by returning the cores to the laboratory intact, but for this study, field examination of the cores was preferable. It avoided any chance of samples being disturbed in transport, examination was easier in daylight, and the core could be related to site conditions which allowed resolution of any queries that arose.

Battery life, and hence the number of rechargeable batteries required, will depend on the depth of forest floor, depth cored into mineral soil and texture of the mineral soil. In particular, penetration of clay mineral soil requires full power, which can rapidly drain the battery. At one extreme, coring through deep *P. tremuloides* forest floors and 15 cm into underlying clay could drain a battery in as few as 10 cores. At the other extreme, one battery was sufficient for 30-40 cores in *P. banksiana* forests where there were thin forest floors over sandy mineral soil.

It is important that the corer be kept sharp. In normal use, it was necessary to sharpen the edge every 20-30 cores. As noted above, this can be done with the drill and a rotary sanding disc, or with a sharpening stone for a light touch-up. When sharp, the corer slices cleanly through virtually all forest floor materials, including roots up to 2-cm thick. It is possible to cut through thicker roots, but the battery drain becomes excessive. The corer is not suitable for stony soils or for soils where bedrock is close to the surface as the cutting edge is easily dulled; if in doubt, it is wise to probe the soil with a thin metal rod to determine stoniness or depth to bedrock.

Other applications

The corer system has also been used for three other applications. First, the corer has been effective in obtaining shallow mineral soil samples (down to about 20 cm) for determination of bulk density, organic matter content and water holding capacity. In the stands sampled in the western Canadian boreal forest, it has been noted that fine roots are concentrated in the forest floor and shallow mineral soil, an observation confirmed by Steele et al. (1997). This suggests that the corer would be ideal for investigations of nutrient cycling in these areas, because nutrient release from decomposition and nutrient uptake by roots is occurring in the soil layers that are easily sampled by the corer. The second application was for preliminary evaluations of soil characteristics. The corer is much faster than digging a soil pit and provides a larger and cleaner core than the common 22 mm soil probe. When the core is laid in the examining tray, layers and horizons are clearly visible as are other characteristics such as soil colour, mottles, fire scars, and fine roots. The third application is taking increment cores from trees, albeit with a standard increment borer tube instead of the two-inch water pipe and an appropriate adaptor. The concept is similar to a previously described borer powered by a chainsaw motor (Hall and Bloomberg, 1984), but the battery-powered drill is much lighter, is easier to operate, has no exhaust fumes and virtually no fire risk. It provided adequate power for trees in the western Canadian boreal forest where increment cores are seldom longer than 25 cm. Apart from the advantage of speed, this "powered borer" enables cores to be taken at ground level, which is important for reducing uncertainty when trees are being aged.

Sampling considerations

Methods

The corer was used to determine stand level values of forest floor organic matter and bulk density, as well as moss/lichen layer biomass and bulk density. These means were used for a forest floor dynamics study (Nalder and Wein, 1999). Here the objective is to present stand level variability data from 114 upland stands across the western Canadian boreal forest. Stands were dominated by *P. glauca*, *P. tremuloides* or *P. banksiana*. In each stand, 10 cores were taken at five-metre intervals along a randomly-oriented sampling transect. Cores were taken vertically through moss/lichen and the forest floor and 15-20 cm into mineral soil. When cores could not be taken at the designated spot because of logs, large roots or rocks, the corer was moved 50 cm further along the transect. The depth of each layer was recorded. Compression of the sample was routinely checked by comparing the length of the core in the examining tray against the depth cored. The moss/lichen layer was removed at the top of the litter layer, which was essentially at the base of the photosynthesising tissue. As the study was interested in forest floor accumulations since the last stand-replacing fire, the base of the forest floor layer was defined by the midpoint of the fire scar or at the mineral soil surface if no fire scar was discernible. Forest floor samples were air-dried, woody matter was chopped into small fragments, the sample was ground until suitably homogenous, and a subsample of approximately 5 g was taken. This subsample was oven-dried to constant weight at 75 °C, then ashed at 450 °C for 16 hours to determine organic matter content and percent organic matter. Bulk density was calculated as oven-dry mass divided by volume (cross sectional area of corer by depth of forest floor). Cores containing unusually large accumulations of organic matter, such as rotten logs or squirrel middens, were flagged for separate analysis. Biomass of moss/lichen layer samples was determined by oven-drying to constant weight at 75 °C and bulk density was calculated as for the forest floor.

Results and Discussion

Coefficients of variation (CV) were high for all variables (Table 2-1). This was particularly so for moss-plus-lichen biomass, where CV's were close to 80%, mainly because many cores had no moss or lichen, i.e., moss or lichen cover tended to be patchy. For forest floor variables, CV's were on average about 30% (Table 2-1). Values for *P. banksiana* were generally much higher than the other two species, and values for organic matter and bulk density were higher than those for depth and percent organic matter. The variability in percent organic matter was surprisingly high, and is likely due to the unavoidable inclusion of small amounts of mineral soil with each forest floor sample. Similar CV's for forest floor variables have been reported elsewhere. In *Pinus sylvestris*, there is a CV of 27% for C density (kg m^{-2}) of the F-H layer (Liski, 1995) and 32% for H-layer thickness (Finer et al., 1997). Across a range of forest types in the northern United States, Grigal et al. (1991) report a CV of 30% for percent organic matter. The latter study noted that variability was correlated with means, which is also evident in here (Figure 2-3). The linear relationship between standard deviations and means for each species indicates that CV's remain fairly constant over a wide range of means.

Data in Table 2-1 will tend to be conservative because unusually deep forest floor cores, particularly those through rotten logs, were excluded from this analysis. Considering forest floor organic matter as an example, inclusion of the excluded cores increases CV's to 37, 47 and 34% for *P. glauca*, *P. banksiana* and *P. tremuloides*, respectively. Depending on the purpose of the study, it may or may not be desirable to treat these cores separately; for the forest floor dynamics study, it enabled separation of components whose dynamics were quite different (Nalder and Wein, 1999).

What are the implications of these high CV's for sampling intensity? For the forest floor dynamics study, 10 samples per stand proved adequate to detect the hypothesized effects of age, species and climate on forest floor accumulation (Nalder and Wein, 1999). In Finland, Liski (1995) recommends 8-10 samples per stand for studying organic layer and mineral soil dynamics. As illustrated by Figure 2-4, however, the number of samples is very sensitive to the desired relative standard error (RSE), defined as the standard error of the mean ($S_{\bar{x}}$) as a percentage of the mean. This may vary considerably depending on the objectives of the study. At one extreme, 100 samples (RSE=3% with a CV of 30%), would probably be insufficient for detecting year-to-year changes in forest floor C pools because long-term accumulation rates are generally less than 1% per year (Nalder and Wein, 1999). At the other extreme, RSE's of 20% have been suggested as adequate for wildfire fuel load studies (Brown, 1974; Van Wagner, 1982) so that three samples per stand may suffice. This assumes normally-distributed data, which was not true for any variable based on the Lilliefors test at 5% significance level (SPSS Inc., 1993). Rather, all variables except percent organic matter were log-normally distributed. As shown by Grigal et al. (1991), fewer samples are required for the same precision under the log-normal assumption.

It may be possible to reduce variability by sampling with a larger cross-sectional area, such as the traditional 30-cm square template. Certainly the integrating effect of 900 cm^2 has an intuitive appeal compared with the 22 cm^2 of the corer presented here. It has been observed, however, that forest floor variability is small over a scale of centimetres compared with a scale of meters. In support of this, organic layer accumulation is greater under canopies or close to tree stems (Hokkanen et al., 1995; Liski, 1995) which in most stands provides a patterning on the scale of meters. Consequently, it is doubtful that a larger cross-sectional area would have a significant impact on sampling variability. If so, then the sampling efficiency (defined as $1/(n^*t)$, where *n* is the number of samples required and *t* is the time taken for each sample) will be much lower for large template methods.

Spatial autocorrelation may lead to bias in estimates, particularly if sampling intervals are small compared with the scale of variation. Spatial autocorrelation was tested with two methods using forest floor organic matter as an indicator variable. First, autocorrelation coefficients were calculated for lags ranging from 1 to 8 and tested for significance at the 5%

level using the Box-Ljung statistic (SPSS Inc., 1993). Of the 114 stands sampled, only seven showed evidence of autocorrelation, defined as having more than one significant lag interval. Three other stands had one significant lag interval, but given the large number of tests performed, this is to be expected by chance alone. Among the seven stands, there was no apparent pattern. Two were *P. glauca*, two were *P. banksiana*, three were *P. tremuloides*, and they spanned a wide range of ages and stem density, suggesting that the apparent autocorrelation was due to chance. The second method was a semivariogram analysis, a technique commonly used in geostatistics (Kitanidis, 1997). For each stand, semi-variances were calculated for lags from 5 to 35 m at five-metre intervals. Because there were insufficient points in each stand to develop a stable variogram, semi-variances were normalized by expressing them as a fraction of the stand mean, then the normalized semi-variances were averaged across all stands. Again there was little evidence of spatial autocorrelation: the composite semi-variogram indicates variability is fairly constant with distance (Figure 2-5). This is consistent with two studies in *Pinus sylvestris* stands. In one, there was no clear spatial dependence over intervals of 5-50 m (Hokkanen et al., 1995), and in the other, spatial dependence occurred mainly at distances less than 5 meters (Liski, 1995). It is concluded that spatial autocorrelation was not a concern with the 5-m sampling intervals used in this study.

Spatial variability is just one component of variation leading to the high CV's in Table 2-1. Here three other sources are considered, corer bias, layer separation error and core compression. Corer bias may occur for two reasons. First the corer never makes a perfect vertical cross section through sampled layers; as noted previously, the cutting edge may push some material aside, or capture some material that is outside the cross sectional area, or be diverted by hard objects. This effect cannot be quantified, but qualitatively it is judged to be insignificant given the clean cut made by the corer. Second, not all chosen points along the transect can be cored because of obstructions, particularly large logs representing the boles of fallen trees. This may bias estimates if forest floor characteristics are different at these points. To illustrate, large logs obstructed 112 of the 1252 sampling points in this study. Because logs tend to screen the underlying ground from litterfall, it is likely that the forest floor is thinner under logs. Assuming a 50% reduction, estimates of mean forest floor organic matter would overestimate actual values by about 5%. Clearly, there is a potential for significant bias.

The second potential source of error occurs because identification and separation of layers is never precise; layers often inter-grade and estimation of a layer boundary has an element of subjectivity. Assigning layer boundary to the nearest 0.5 cm was as precise as was warranted, even with the good quality cores produced by this corer. This imprecision can represent a significant source of error, particularly in thin layers. Next to spatial variability, this was judged to be the next largest component of variability, and it probably accounts for the higher CV's in *P. banksiana* (Table 2-1).

The third potential source of error is core compression which effects bulk density. Significant compression can occur, particularly with the moss-lichen layer, if the corer is not sharp or if the drill is pushed down while coring. However, with a sharp corer and the proper coring technique, no core compression was observed, so it is doubtful that this would be significant source of variation.

Conclusion

An effective device for sampling forest floors has been described, which is also useful for other layers. It is easy to fabricate, inexpensive, allows cores to be taken rapidly by one person, and gives undisturbed, natural-volume cores when coring through materials as varied as moss, lichen, litter, ferment, humus and mineral soil. Sampling CV's for forest floor organic matter and bulk density were typically 30% or higher. Most of this variation is attributed to spatial variability although the lack of precision in identifying layer boundaries undoubtedly forms a significant component, particularly for thin layers. The impact of logs is not insignificant and needs to be considered. It is clear that high precision is not feasible in forest floor sampling. For a study of forest floor dynamics, 10 samples per stand gave adequate precision and this seems to be sufficient for many studies. Obtaining more precise estimates would soon become very expensive in sampling effort. These data support the choice of five-metre sampling intervals as adequate to avoid spatial autocorrelation.

Acknowledgements

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Tables

Table 2-1. Mean coefficients of variation for within-stand variation for several variables (mean CV ± standard deviation of CV, number of stands in parentheses).

Variable	*P. glauca*	*P. banksiana*	*P. tremuloides*
Forest floor			
Organic matter (kg m^{-2})	34%±13% (23)	38%±14% (42)	29%±9% (49)
Bulk density (Mg m^{-3})	32%±11% (17)	53%±29% (36)	32%±12% (47)
Percent organic matter	21%±7% (23)	37%±17% (42)	21%±8% (49)
Depth (cm)	30%±15% (17)	44%±14% (36)	22%±7% (48)
Moss-plus-lichen			
Biomass (kg m^{-2})	75%±51% (23)	81%±40% (37)	NA[1]
Bulk density (Mg m^{-3})	42%±17% (17)	45%±15% (33)	NA[1]

[1] No moss-plus-lichen data are given for *P. tremuloides* because occurrence of moss or lichen was rare in these stands.

Figures

Figure 2-1. Use of corer system to take a forest floor sample: a) coring, b) extracting core onto examining tray.

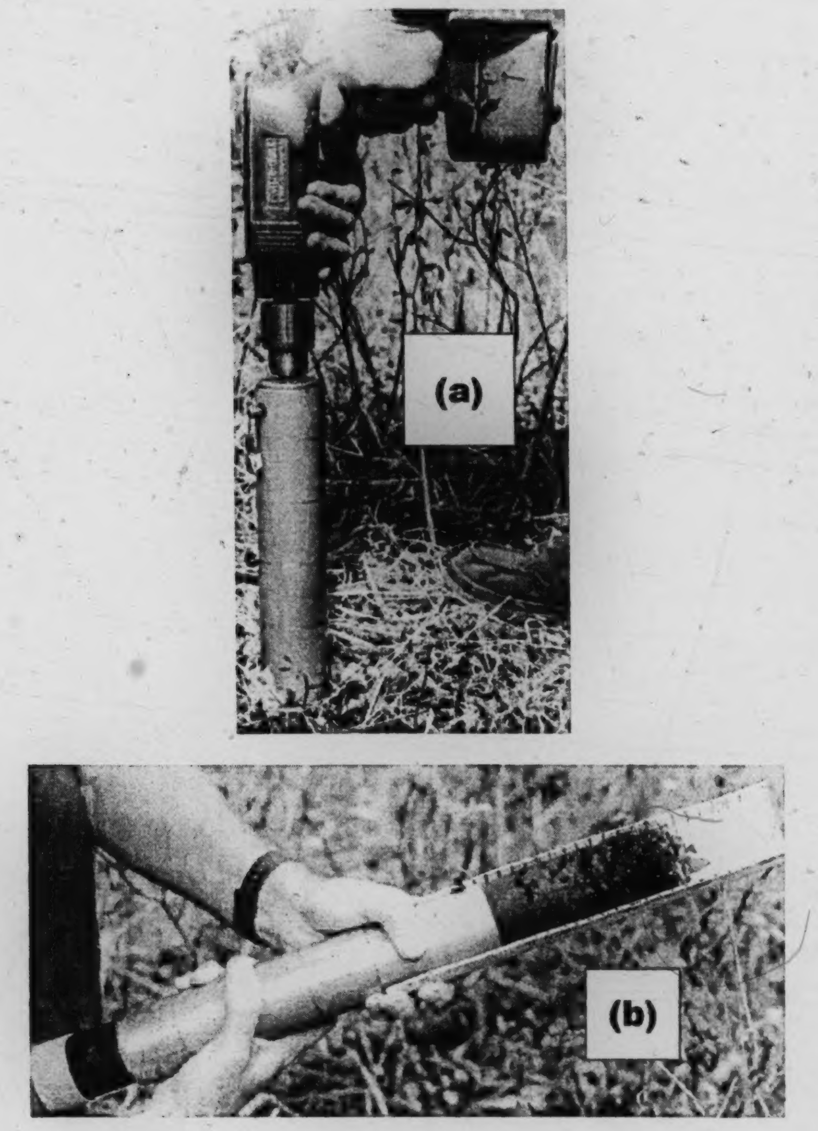


Figure 2-2. Corer and adaptor unit.

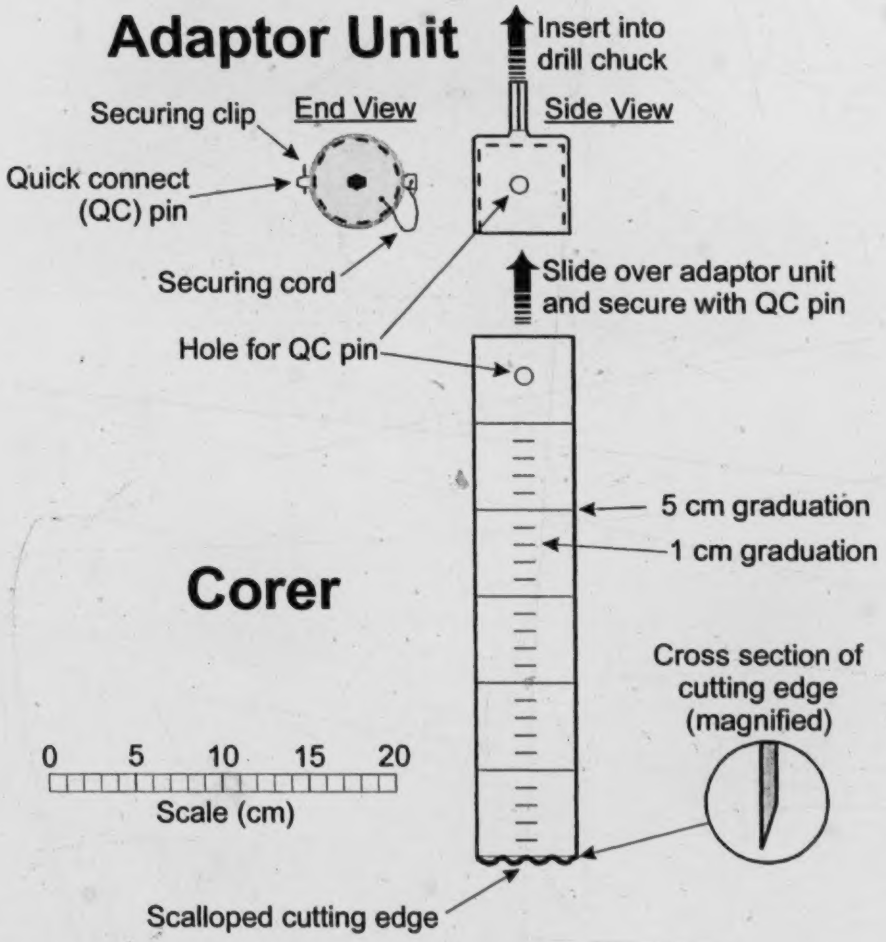
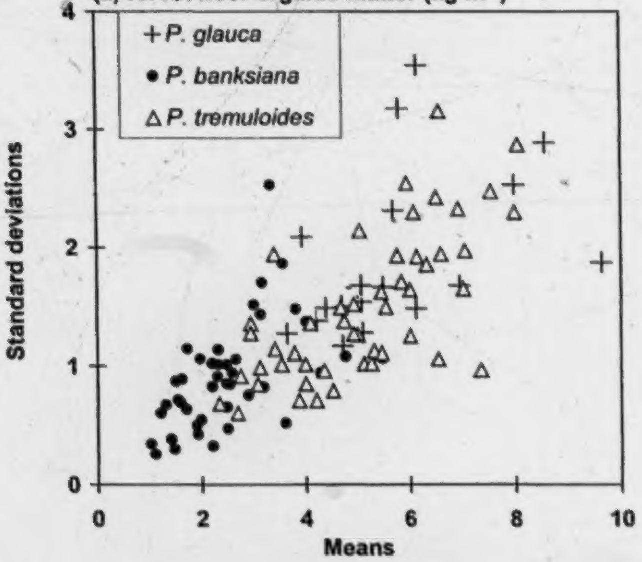

Adaptor Unit
Insert into drill chuck
Securing clip
End View
Side View
Quick connect (QC) pin
Securing cord
Slide over adaptor unit and secure with QC pin
Hole for QC pin
5 cm graduation
1 cm graduation
Corer
Cross section of cutting edge (magnified)
0
5
10
15
20
Scale (cm)
Scalloped cutting edge

Figure 2-3. Linear relationships between means and standard deviations: a) forest floor organic matter, b) forest floor bulk density.


(a) forest floor organic matter (kg m^{-2})

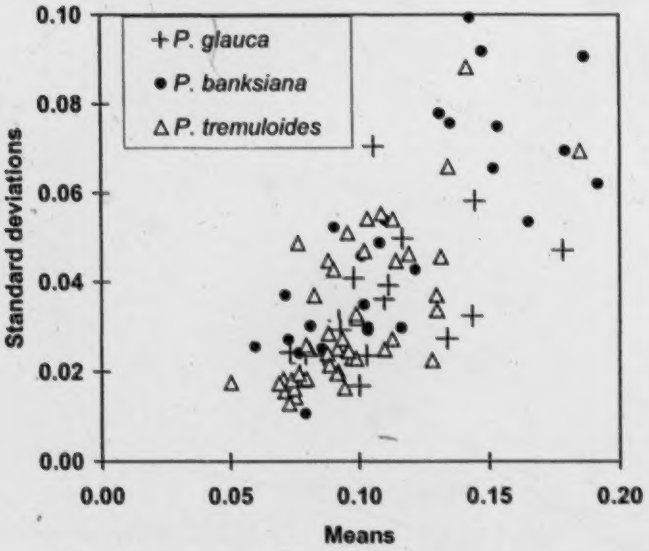

(b) forest floor bulk density (Mg m^{-3})

Figure 2-4. Relationship between relative standard error (RSE) and number of samples (N) for a range of coefficients of variation (CV) assuming a normal distribution (RSE = CV / √N *100 %).

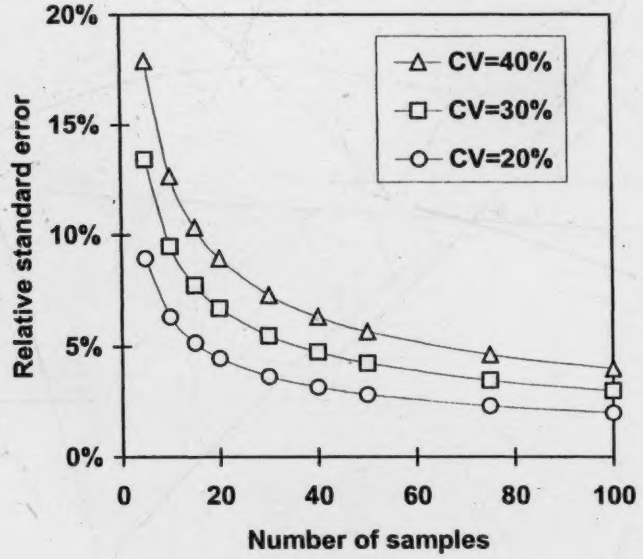
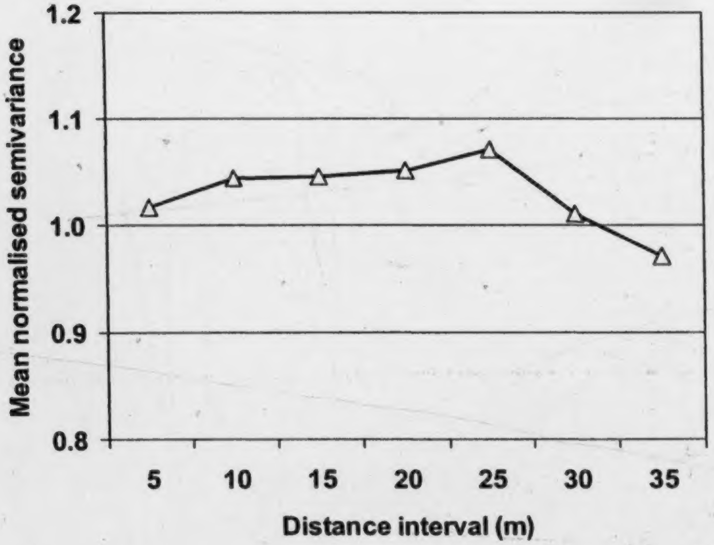


Figure 2-5. Semi-variogram showing spatial variability along sampling transect, averaged across 114 stands.



References

Agriculture Canada Expert Committee on Soil Survey 1987. The Canadian System of Soil Classification. Publ. 1646. Agric. Can., Ottawa, Ontario.

Alban, D.H. 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. Soil Sci. Soc. Am. J. 46: 853-861.

Bonan, G.B. and Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Sys. 20: 1-28.

Brown, J.K. 1974. Handbook for inventorying downed woody material. Gen. Tech. Rep. INT-16. Intermountain Forest and Range Experimental Station, USDA For. Serv., Ogden, Utah.

Finer, L., Messier, C. and De Grandpre, L. 1997. Fine-root dynamics in mixed boreal conifer--broad-leafed forest stands at different successional stages after fire. Can. J. For. Res. 27(3): 304-314.

Forestry Canada Fire Danger Group 1992. Development and structure of the Canadian Forest Fire Behaviour Prediction System. Inf. Rep. ST-X-3. Forestry Canada, Ottawa, Ontario.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J. and Stow, T.K. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophy. Res. 102(D24): 29029-29041.

Grigal, D.F., McRoberts, R.E. and Ohmann, F.F. 1991. Spatial variation in chemical properties of forest floor and surface mineral soil in the north central United States. Soil Sci. 151: 282-290.

Hall, A.A. and Bloomberg, W.J. 1984. A power-driven increment borer. For. Chron. 60(6): 356-257.

Hokkanen, T.J., Jarvinen, E. and Kuuluvainen, T. 1995. Properties of top soil and the relationship between soil and trees in a boreal Scots pine stand. Silva Fennica 29(3): 189-203.

Huang, W.Z. and Schoenau, J.J. 1996. Forms, amounts and distribution of carbon, nitrogen, phosphorus and sulfur in a boreal aspen forest soil. Can. J. Soil Sci. 76: 373-385.

Johnson, D.W. 1995. Role of carbon in the cycling of other nutrients in forested ecosystems. In: McFee, W.W. and Kelly, J.M. (Eds.). Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Inc., Madison, Wisconsin. pp. 299-328.

Kimmins, J.P. 1987. Forest Ecology. Macmillan Publishing Company, New York. 531 pp.

Kitanidis, P.K. 1997. Introduction to Geostatistics: Applications in Hydrogeology. Cambridge University Press, Cambridge. 249 pp.

Liski, J. 1995. Variation in soil organic carbon and thickness of soil horizons within a boreal forest stand - effect of trees and implications for sampling. Silva Fennica 29(4): 255-266.

Liski, J. and Westman, C.J. 1997. Carbon storage in forest soil of Finland: 2. Size and regional patterns. Biogeochem. 36: 261-274.

Nalder, I.A. and Wein, R.W., 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochem. Cycles, 13(4): 951-968.

Nalder, I.A. and Wein, R.W., 1998. A new forest floor corer for rapid sampling, minimal disturbance and adequate precision. Silva Fennica, 32(4): 373-382.

Paré, D. and Bergeron, Y. 1996. Effect of colonization tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Can. J. For. Res. 26(6): 1022-1031.

Quintilio, E., Alexander, M.E. and Ponto, R.L. 1991. Spring fires in a semimature trembling aspen stand in central Alberta. Inf. Rep. NOR-X-323. Can. For. Serv., Edmonton, Alberta.

SPSS Inc. 1993. SPSS for Windows: Base System User's Guide, Release 6.0. SPSS Inc., Chicago, Illinois, 828 pp.

Steele, S.S., Gower, S.T., Vogel, J.G. and Norman, J.M. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17: 577-587.

van Cleve, K. and Noonan, L.L. 1971. Physical and chemical properties of the forest floor in birch and aspen stands in interior Alaska. Soil Sci. Soc. Am. Proc. 35: 356-360.

van Cleve, K., Olivier, L., Schlentner, R., Viereck, L.A. and Dyrness, C.T. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. 13: 747-766.

Van Wagner, C.E. 1982. Practical aspects of the line intersect method. Inf. Rep. PI-X-12. Can. For. Serv., Edmonton, Alberta.

Van Wagner, C.E. 1983. Fire behaviour in northern conifer forests and shrublands. In: Wein, R.W. and McLean, D.A. (Eds.). The Role of Fire in Northern Circumpolar Ecosystems. John Wiley and Sons, Chichester. pp. 65-80.

Westman, C.J. 1995. A simple device for sampling of volumetric forest soil cores. Silva Fennica 29(3): 247-251.

Zackrisson, O., Nilsson, M.-C., Steijlen, I. and Hörnberg, G. 1995. Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. J. Ecol. 83: 469-483.

3. Spatial interpolation of climatic Normals: test of a new method in the Canadian boreal forest[2]

Introduction

The long-term dynamics of forests are commonly simulated to examine aspects such as growth and yield, succession, carbon dynamics and nutrient cycling. Climatic information is usually required for the sites being simulated, but long-term records are rarely available for specific sites, so as a surrogate, regional climate data from nearby climate stations are frequently utilized (Running et al., 1987; Bradley et al., 1995; Nalder and Merriam, 1995; Sykes and Prentice, 1995; Bugmann and Fischlin, 1996; Talkkari and Hypén, 1996; Liski and Westman, 1997; Peng et al., 1998). Either the assumption is made that the climate recorded at a given climate station is representative of the surrounding region, or else climate variables are spatially interpolated to generate data for a specific site or for a series of grid cells.

Spatial interpolation becomes particularly problematic when climate stations are few and widely separated. This is the case for much of the boreal forest of Canada, where climate stations can be separated by hundreds of kilometres. The region of interest (Figure 3-1) is defined by a separate study of forest floor dynamics for which 121 forest stands were sampled across northern Manitoba, Saskatchewan, Alberta and the southern Northwest Territories. This region, referred to here as the western Canadian continental boreal forest (WCCBF), is relatively homogeneous, having low relief and broadly similar vegetative cover and land-water ratios. Given this uniformity, it was hoped that a method could be found that was simple to apply and would give good estimates for the study sites despite the limited number of climate stations.

Interpolation methods commonly applied to estimating temperature or precipitation include distance weighting (Tabios III and Salas, 1985; Eischeid et al., 1995; Lennon and Turner, 1995; Ashraf et al., 1997; Dodson and Marks, 1997), interpolating polynomials (Stewart and Cadou, 1981; Tabios III and Salas, 1985; Eischeid et al., 1995; Lennon and Turner, 1995), kriging (Tabios III and Salas, 1985; Phillips et al., 1992; Hammond and Yarie, 1996; Holdaway, 1996; Ashraf et al., 1997) and splines (Hulme et al., 1995; Lennon and Turner, 1995). Distance weighting, which estimates the variable of interest by assigning more weight to closer points, is the simplest technique. Interpolating polynomials fit a polynomial of an appropriate degree to the data points: higher degree polynomials provide a better fit, but may give totally unreasonable values between data points. Kriging, originally developed for mining ore estimation, assigns weights to minimize the variance and bias of the estimates. Spline methods, which are equivalent to kriging with a generalized covariance function (Cressie, 1986), fit polynomials to a restricted set of points to provide a smooth, minimum curvature surface passing through the points.

Several climate interpolations have been done for specific regions of western Canada (Longley, 1972; Longley and Janz, 1978; Stewart and Cadou, 1981; Olson, 1986; Hogg, 1994;

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[2] A version of this chapter has been published. Nalder and Wein 1998. Agricultural and Forest Meteorology. 92:211-225.

Halsey et al., 1995) but none of these have attempted to define an optimal method of interpolation. There is little evidence that any one method is optimum across a range of conditions: rather it is important to determine the best method for each circumstance (Lennon and Turner, 1995).

For the region of interest, a simple, robust and flexible method of estimating temperature and precipitation at specific sites was required. Kriging has the advantages that it is a well proven technique, software is readily available, it provides optimal interpolation in the sense of providing the best linear unbiased estimate, it provides error estimates at the unknown points, and since it can return the original data values, it can be considered an exact technique. However, it assumes stationarity of data, which is almost never true. This assumption can be relaxed with specific forms of kriging, but it still has to be determined which form is applicable to a particular data set. Additionally, definition of the required variogram models (see Methods) is time consuming and somewhat subjective. Definition of neighbourhoods (the area outside which stations are not used in the kriging process) is also required which is difficult to do objectively. Consequently, testing some simple alternatives to kriging was of interest, as well as testing the various forms of kriging, to determine the most suitable method for interpolation in this region.

Methods

Climatic data

Spatial interpolation of mean monthly temperature (T) and mean monthly precipitation (P) was carried out using 30-year averages, termed Normals, for the period 1961 to 1990 (Environment Canada, 1994). The boundary of the study region (Figure 3-1) was drawn primarily to encompass the 121 stands previously mentioned while avoiding agricultural land to the south, Hudson Bay to the east, the Rocky Mountains to the west and the transitional forest to the tundra in the north. Within this region, 31 climate stations were identified that had complete monthly temperature and precipitation Normals data for 1961-1990. Of these 31 stations, two were excluded (Hay River and Cree Lake) that were located on the shores of large lakes. These were excluded because none of 121 stands were located close to large lakes, and although the lake influence can be considerable, it is generally localized (Holdaway, 1996). Three additional stations were available with precipitation Normals. The locations of the 32 stations used in this analysis are shown in Figure 3-1. They range in elevation from 145 to 633 m a.m.s.l. with elevation generally increasing towards the southwest.

Latitude, longitude and elevation of each climate station were taken from Environment Canada (1994). Since the kriging software used calculates planar distances, latitude and longitude were transferred to a planar co-ordinate system following Ashraf et al. (1997). To do this, great circle distances (km) and bearings to each climate station were calculated from a central, reference point (57°N, 105°W), then this polar representation was converted to X-Y, which was offset by 750 and 500 km, respectively, so that all distances were positive.

Logarithmic transforms of precipitation can give a more normal distribution and/or improved predictions (Stewart and Cadou, 1981; Phillips et al., 1992; Daly, 1994). Examination of the monthly precipitation data, however, revealed that it was not significantly different from a normal distribution at the 5% level using the Kolgorov-Smirnov test for 9 of the 12 months and that log-transformed data made no difference to this result. As a further check, cross validation errors were calculated using method 7 (see below) with both raw data and log-transformed data: the log transforms gave slightly higher errors. Consequently, untransformed data were used throughout the analysis.

Kriging - general

Four of the interpolation methods are variants of the basic kriging procedure. Cressie (1991) and Kitanidis (1997) give detailed treatments of kriging. The basis of kriging is the semi-variogram, usually referred to as a variogram, which defines variation as a function of distance:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{k=1}^{N(h)} \left[Z(x_k + h) - Z(x_k) \right]^2 \qquad (1)$$

where $\gamma(h)$ is the semi-variance of variable Z at separation distance h and $N(h)$ is the number of pairs of points in the distance interval $h + \Delta h$. Values are calculated for each possible pair of stations and the mean values of the semi-variance are plotted for successive distance intervals to produce the experimental variogram. A model variogram is fitted to these points, and this model is used in generating an autocovariance matrix. Estimates for the test sites are calculated by summing weighted values for each climate station where the weights are determined so that $E\{Z^*(x_0)-Z(x_0)\}=0$ and the estimation variance $\mathrm{Var}\{Z^*(x_0)-Z(x_0)\}$ is minimized. For co-kriging, the cross-semi-variance for the two variables of interest is calculated by:

$$\gamma_{12}(h) = \frac{1}{2N(h)} \sum_{k=1}^{N(h)} \left[Z_1(x_k + h) - Z_1(x_k) \right] \left[Z_2(x_k + h) - Z_2(x_k) \right] \qquad (2)$$

where Z_1 is the first variable and Z_2 is the second variable.

Variogram models were developed for each month for (1) Temperature, (2) Precipitation, (3) Elevation, (4) Residuals of temperature after detrending, (5) Residuals of precipitation after detrending, and (6) Cross-variograms of temperature-elevation and precipitation-elevation. The application of each is discussed below. In each case, the experimental variogram was examined and the most suitable type of model, e.g., Gaussian, was selected by eye, then the model was fit to the data points using weighted least squares fit (Cressie, 1985). Experimental variograms were plotted using distance intervals of 100 km and a maximum distance of 1200 km.

Anisotropy was also investigated by generating variograms and fitting models at 22.5 degree intervals with a tolerance of ±22.5 degrees. To enable comparisons between directions, the same model form must be used throughout. A linear model was chosen because the limited number of data points in each arc made it unrealistic to define more complex models. Use of a linear model precludes using the conventional anisotropy ratio (the ratio of the range in the major direction of continuity to the range in a direction perpendicular to the major direction (Phillips et al., 1992; Pebesma, 1997)), therefore anisotropy ratio (AR) is calculated as:

$$AR = \max\left\{ \frac{C_1(\theta)}{C_1(\theta + 90)} \right\}, \theta = 0, 22.5, 45 \ldots 180 \qquad (3)$$

where C_l is the slope coefficient of the fitted linear model and θ is the angle assessed with the directional variogram.

The Gstat software package was used for generating experimental variograms, fitting variogram models and performing kriging estimates (Pebesma and Wesseling, 1998). Visual Basic™ for Applications (VBA) programs were written to generate the required data and command files for Gstat, as well as to read and summarize the output files.

Method 1 - Ordinary kriging

Ordinary kriging estimates the value of a climatic variable at a point from its values at surrounding stations and a variogram model for that variable. The spatial vector is formed from X and Y co-ordinates. Second order stationarity is assumed, i.e., the variogram function depends on the separation vector, not on location (Journel and Huijbregts, 1978) which requires that there is no trend in the data. This is seldom the case, but may be an acceptable assumption if the points used in the interpolation are restricted to a relatively small neighbourhood (Holdaway, 1996). In Gstat, the neighbourhood can be defined by setting a maximum distance and/or minimum and maximum number of stations. To determine an optimum neighbourhood, temperature data was arbitrarily selected for the first month (January) and cross validation errors were calculated (see below) for a range of neighbourhood constraints. A maximum distance of 300 km, which provided at least three stations, combined with a maximum limitation of eight stations, gave the lowest errors. This neighbourhood was also used for the co-kriging and detrended kriging (methods 2 and 3).

Method 2 - Co-kriging

Co-kriging takes advantage of the correlation between two variables, in this case the climatic variable and elevation. Three variogram models were used for each run: 1) climatic variable, 2) elevation and 3) cross-variogram of the climatic variable and elevation. The spatial vector is formed from X and Y co-ordinates and elevation is a co-variate.

Method 3 - Detrended kriging

To better meet the assumptions of stationarity, a multiple linear regression of *T* and *P* against X, Y and elevation was carried out to remove first order trends. The residuals were used to generate new variograms and then ordinary kriging was carried out on these residuals. The resulting estimates were added to the trend to give the *T* or *P* estimates. This method has been termed residual kriging (Holdaway, 1996), kriging with trend model (Journel and Huijbregts, 1978) and detrended kriging (Phillips et al., 1992). The latter term is used here.

Method 4 - Universal kriging

Universal kriging (Ver Hoef, 1993) also takes account of trends in the data by removing trends apparent within the kriging neighbourhood. The variogram model previously generated for *T* or *P* was used and a first order trend model using X, Y and elevation as independent variables was specified. The results remain sensitive to neighbourhood, although less than with ordinary kriging. Again, January temperature data was used to test for sensitivity and a radius of 600 km with a maximum of 10 stations gave the lowest errors. This neighbourhood was used for the remaining universal kriging runs.

Method 5 - Nearest neighbour

The nearest neighbour method uses climatic data from the nearest climate station to estimate the value at a test site. It is not strictly interpolation, but essentially tests the assumption that a climate station is representative of an area, where the area is formed from all points that are closer to the station than to any other station. It is also known as the Thiessen polygon method (Tabios III and Salas, 1985). It is the simplest method and provided a baseline for testing improvements offered by the other methods. VBA programs were written to carry out the computations for this method as well as for methods 6 and 7.

Method 6 - Inverse distance squared

The inverse distance squared method averages the climate variable from surrounding stations with more weight given to those that are closest. The weighting function is the inverse square of the distance, so that the predicted value for a site is given by:

$$Z=\left[\sum_{i=1}^{N}\frac{Z_i}{d_i^2}\right]\Big/\left[\sum_{i=1}^{N}\frac{1}{d_i^2}\right] \quad \text{.......(4)}$$

where Z is the estimated climatic variable (T or P), Z_i is the value at climate station "i", d_i is the distance from the site to climate station "i" and N is the number of climate stations used for the interpolation.

Method 7 - Gradient plus inverse distance squared

The same multiple linear regressions developed for detrended kriging were also used to define climatic gradients as X, Y and elevation coefficients. These gradients were then used to predict each climate variable for each test site based on the remaining stations. The values so obtained (N_T=28, N_P=31) were averaged using inverse distance squared weighting:

$$Z=\left[\sum_{i=1}^{N}\frac{Z_i+(X-X_i)*C_x+(Y-Y_i)*C_Y+(E-E_i)*C_E}{d_i^2}\right]\Big/\left[\sum_{i=1}^{N}\frac{1}{d_i^2}\right] \quad \text{.......(5)}$$

where X and X_i are the X co-ordinates of the test site and climate station "i" respectively, Y and Y_i are the Y co-ordinates of the test site and climate station "i" respectively, E and E_i are the elevations of the test site and climate station "i" respectively, and C_x, C_y and C_e and regression coefficients for X, Y and elevation respectively.

This method is termed "gradient-plus-inverse distance squared" (GIDS). It has not been used before. It was attractive because it seemed to explain much of the variation in the data set while being easy to implement: the necessary calculations can be performed in a simple spreadsheet.

Assessment criteria

As a test of the accuracy of each method, T or P was calculated for each climate station after excluding that station from the input data. This is a common validation method in climate studies and has variously been termed "cross validation" (Hulme et al., 1995; Holdaway, 1996), "jack knifing" (Phillips et al., 1992; Daly, 1994), and "fictitious point" (Tabios III and Salas, 1985; Ashraf et al., 1997). The term cross validation is used here. A more rigorous test would be to reserve a certain number of stations for validation as per Hulme et al. (1995), but given the limited number of stations in the study region, this was not practicable.

For each method and each month there were 29 observations for temperature and 32 for precipitation. Error was calculated as "actual minus predicted" and the mean of these errors was calculated in three ways following Hulme et al. (1995): mean error (ME), mean absolute error (MAE) and root mean square error (RMSE). ME indicates the degree of bias, MAE provides a measure of how far the estimate can be in error, ignoring sign, and RMSE provides a measure that is sensitive to outliers. Differences among methods were tested using a two tailed *t*-test for paired samples: MAE was used as the response variable because the primary interest of this study concerned the absolute magnitude of likely errors for sensitivity testing of a forest growth model. The method that gave the lowest MAE was paired with each of the remaining methods.

Results

Variograms

For each month and each variable, five variogram models were generated for a total of 120 models. Ordinary and universal kriging utilized the same model. Detrended kriging required a separate model based on residuals. Co-kriging required a model for each variable plus a third model to characterize their covariance. Of the 120 models, 70 were linear, 38 were Gaussian, 10 were spherical and 2 were power. Model forms are defined in Pebesma (1997) .

There was considerable variation in the variogram models among months (Figure 3-2). For temperature, models generally provided a good fit to the experimental variogram. The fit for co-kriging models was constrained by the need to use a common model type and range for the three variograms, but in general good fits were obtained. The models for precipitation provided poorer fits than for temperature, particularly for co-kriging where it was seldom possible to find a model type and range that provided good fits for the three variograms. Twelve models had negative slopes, e.g., January precipitation in Figure 3-2.

Anisotropy

Strong anisotropy was evident in both temperature and precipitation data with T having consistently higher anisotropy ratios (AR) than P (Table 3-1). AR values above 1.0 indicate some degree of anisotropy. For both T and P, anisotropy varied considerably over the year. For T, the direction of major variance was NE-SW from April to August and NNE-SSW for the remaining months, but for P it was more variable, from N-S to ESE-WNW. The directional variograms also showed a strong seasonal trend in variance, with T variance being very low in summer, but P variance being low in winter months.

Gradients

The multiple linear regressions carried out for GIDS and detrended kriging methods revealed strong gradients in the climatic data which varied by month in a fairly consistent manner. Figure 3-3 plots the T and P coefficients for X, Y and elevation, together with r^2 values, with all stations included in the regression. All T coefficients, except those for elevation in March, October and November, were significant at the 5% level. For P, the gradients were neither as strong nor as significant: 16 of the 36 coefficients were not significant at the 5% level. Consistent seasonal patterns, however, were still evident. In contrast to T, the highest r^2 occurred during the summer. Second order terms were tested but the improvements in r^2 were only slight.

Cross validation errors

A summary of the errors obtained from the cross validation tests is presented in Table 3-2. Mean error is relatively low for all methods, but is generally lowest for kriging. For both T and P, the GIDS method gave the lowest MAE and RMSE. The lowest ME was obtained with detrended kriging for T and universal kriging for P. Ordinary kriging gave consistently poor performance. When methods were ranked, the ranking was the same for both MAE and RMSE. With the exception of universal kriging of P, RMSE was only slightly higher than MAE, indicating that the methods were not susceptible to extreme errors.

For all methods, there was substantial variation in error across the year (Figure 3-4). For temperature, the highest errors occurred in winter and the lowest values from June to October, which probably reflects the greater temperature differences across the region in winter, e.g., the differences between the warmest and coldest stations are 11.2°C in February compared with 1.4°C in July. In contrast, for precipitation the lowest errors occurred from December through to May.

The GIDS method was used as the baseline when testing for significant differences among the methods. For T interpolation, GIDS was different from all other methods, except detrended kriging, at the 1% level of significance. For P, however, GIDS was only significantly different from detrended kriging (Prob. = 0.0004) and universal kriging (Prob. = 0.01).

Latitude-longitude versus X-Y

A comparison of errors using the GIDS method showed that use of latitude and longitude rather than X and Y co-ordinates increased the MAE from 0.51°C to 0.53°C for temperature and from 3.68 to 3.82 mm for precipitation. The differences in temperature MAE were significant at the 5% level using a two tailed t-test for paired means.

Discussion

Gradients

In the WCCBF, there are strong gradients in T such that much of the variation can be explained by a simple multiple linear regression against station location and elevation. For most months, r^2 was about 0.9 (Figure 3-3) and nearly all terms were significant. Similar high r^2 have been reported in other studies in continental North America (Stewart and Cadou, 1981; Holdaway, 1996; Hogg, 1994).

In all months, temperatures decreased with increasing X and Y, i.e., to the NE. The effect of elevation was more complex: from May to October, the elevation coefficient ranged from -0.005 to -0.01 °C m^{-1}, which brackets the standard adiabatic lapse rate of -0.006°C m^{-1} (Lennon and Turner, 1995), but in winter the coefficient became positive, presumably due to frequent inversions in the region (Longley and Janz, 1978; Olson, 1986). This is in sharp contrast, for instance, to Great Britain, where lapse rates for T range from -0.0059 to -0.0074 °C m^{-1} (Lennon and Turner, 1995). Some studies have used the standard adiabatic lapse rate in predicting monthly temperatures (Leemans and Cramer, 1991; Hammond and Yarie, 1996), but it is clear that would not be appropriate in the WCCBF. Holdaway (1996) noted that elevation is not an important factor in determining temperature outside mountainous areas, but results here contradict this. Elevation was a significant regression term for T in nine months and for P in seven months. Additionally, co-kriging using elevation as a co-variate consistently gave lower errors than ordinary kriging (Table 3-2). Elevation may have a small range in the WCCBF, but it was an important predictor. It is also worth noting that the T coefficient curves for elevation, X and Y approximate sine waves with a period of one year (Figure 3-3). This smooth transition from month to month suggests that temporal interpolation to sub-monthly intervals may be productive.

For precipitation, the regressions explain much less of the variation (Figure 3-3), with an average r^2 of 0.43 and only 55% of the coefficients being significant. In general, P increases towards the NE and with increasing elevation. During the winter months, r^2 is lower and coefficients are close to zero, indicating little predictive power in the regressions.

The gradients in both T and P were confirmed by the directional variograms, which indicated strong temperature trends towards the NE or NNE, and weaker precipitation trends which were somewhat variable in direction but mostly oriented N to NE (Table 3-1). These gradients have important implications for the performance of the various interpolation methods, particularly kriging.

Kriging methods

Ordinary kriging assumes second order stationarity and isotropy, which was clearly not the case here. As noted earlier, they may be acceptable assumptions if the neighbourhood is sufficiently restricted, but even with the relatively small neighbourhood used in this analysis (3-8 stations), the performance of ordinary kriging was generally the worst of the 7 methods (Table 3-2). This was particularly so with T where the gradients were strongest. Holdaway (1996) obtained much lower errors for ordinary kriging of T in Minnesota, reporting a mean square error (MSE) of 0.77 °C^2 versus 5.16 °C^2 from this study. The lower error may be attributable to the smaller area, higher density of stations and availability of 90 years of data in the Holdaway study. However, detrended kriging reduced MSE for this study to 0.51 °C^2 while making virtually no difference in Minnesota, therefore the lower errors in Minnesota are more likely due to the smaller gradients, particularly for elevation. Trends are less of a factor for precipitation and errors from this study were closer to other studies. For example, in the central United States, Tabios III and Salas (1985) found ordinary kriging of annual precipitation gave an MAE of 0.96 inches (24.4 mm) which is slightly higher than the value of 21.4 mm that was obtained by summing monthly errors.

The performance of kriging in this study may be constrained by the limited number of stations. Insufficient data points lead to unstable variograms and may give inappropriate models. Bilonik (1983) suggests 50 as a minimum to obtain a stable variogram. Webster (1992) recommend 150-200 points where variation is isotropic and larger numbers for anisotropic cases. The number of stations used in this analysis (29 for T and 32 for P) would appear sub-optimal, and may explain why good fits were not achieved with many variograms, particularly for precipitation and directional models. If so, this is a limitation of kriging in regions with a sparse coverage of climate stations. It is not clear, however, that poor variogram models will lead to large prediction errors, e.g., Holdaway (1996) noted that temperature errors can be insensitive to the variogram model. Model sensitivity was investigated which revealed that cross validation error estimates in the WCCBF were fairly stable over a range of variogram models, from those that provided a good fit to those that provided a poor fit. Consequently, it is doubtful that the number of stations formed a significant limitation on kriging performance in this study.

Of more concern was the selection of the neighbourhood because cross validation errors were sensitive to this factor. The neighbourhoods used, which were based on a study of January temperatures, are likely not optimal for all runs. Hence the errors may be higher than would have obtained if the neighbourhoods for each variable had been optimized. It is possible to optimize neighbourhoods (and variogram models) by selecting for minimum cross validation error (Phillips et al., 1992). The difficulty with this approach is that it fits the model to the data set and removes the possibility of using cross validation error as an independent test of methods. In the absence of sufficient stations to set aside as test sites, cross validation was the only feasible method of comparison, therefore optimisation through cross validation was ruled out. It should be noted, however, that the results presented for kriging were already partially fit to the data because January *T* data were used to determine the neighbourhoods and data from all stations were used to develop the variogram models. In this sense, the kriging results reported here enjoy an advantage over the other methods that require no *a priori* selection of model parameters.

As with ordinary kriging, co-kriging assumes stationarity so its performance is similarly hampered by the presence of strong gradients. The inclusion of elevation as a covariate, however, was expected to reduce errors because elevation was an important predictor in this region. This turned out to be the case: errors were reduced, particularly for *T*. The relatively slight improvement for *P* may be due to either the poor fit of precipitation variogram models for co-kriging or to the weaker elevational trends.

When spatial temperature trends were taken into account, as with detrended kriging, *T* errors were further reduced (Table 3-2) and the MAE was not significantly different from the method with the lowest overall errors. Precipitation errors, however, were higher than for both ordinary kriging and co-kriging. This result was somewhat surprising, and counter to that of Daly (1994) who reported that detrended kriging of annual precipitation in Oregon gave lower MAE than either co-kriging or ordinary kriging. This may be a consequence of the anomalous behaviour of the residual variograms: five months had high nuggets with negative slopes.

Universal kriging also takes trends into account, but gave higher errors than detrended kriging (Table 3-2). MAE and RMSE for temperature were the second highest of all methods, and those for precipitation were the highest. This poor performance, particularly for precipitation, was unexpected given that Tabios III and Salas (1985) found that universal kriging of annual precipitation gave substantially lower MAE than ordinary kriging in the central United States. The relatively high precipitation RMSE in the WCCBF indicates the presence of some extreme values, which can be seen to occur in October and November (Figure 3-4). Within these two months, inclusion of two stations (Lynn Lake and Whitesands Dam) produced extremely high errors. Removal of these data points reduced MAE and RMSE to a more reasonable 4.31 and 5.74 mm respectively. Both stations are on the northern periphery of the study region and are relatively close together, so it is likely that one (or both) is anomalous resulting in unrealistic weights within the neighbourhood.

Non-kriging methods

Compared with kriging, the simpler methods performed surprisingly well. For both MAE and RMSE, the nearest neighbour method ranked third for temperature and fourth for precipitation (Table 3-2). Interestingly, it gave lower precipitation errors than three forms of kriging, lending support to previous observations (Lennon and Turner, 1995) that more complex methods are not necessarily more accurate.

Inverse distance squared gave slighter lower MAE and RMSE for precipitation than the nearest neighbour method. The errors for temperature, however, were higher and it was the one method where bias (ME) was large enough to be of concern. Apart from bias, it ranked ahead of ordinary kriging and universal kriging for both temperature and precipitation, but this superiority is not reflected in other data sets. In the central United States, inverse distance squared gives higher RMSE than ordinary kriging and co-kriging for interpolation of evapotranspiration (Ashraf et al., 1997) and higher MAE than ordinary kriging and universal kriging for interpolation of annual precipitation (Tabios III and Salas, 1985).

GIDS provided the lowest MAE and RMSE of all methods for both temperature and precipitation. In terms of mean error, it ranked second for temperature and last for precipitation, but these biases were in any case very low.

Seasonal variation

The overall errors, however, hide a much more complex seasonal picture (Figure 3-4). For instance, ordinary kriging, which gave poor overall performance, gave the lowest errors for November *T* and for *P* in March, July and August. Across the year, no one method is consistently best. GIDS is the most consistent, although its performance for *P* from July to September is poor. This might suggest that methods should be chosen on a month by month basis, but this approach is rejected for two reasons. First, at the monthly level of aggregation, significant differences that will clearly establish the preferred approach are less likely. Second, the objective of the study was to find a single method of interpolating climate across the WCCBF: mixing and matching methods would seriously complicate the analysis.

Selected method

The GIDS method gave the lowest MAE and RMSE while providing low ME's. It was robust in that it provided the lowest MAE and RMSE for two data sets with very different characteristics (*T* and *P*), and from month to month it gave more consistent performance than any other method. It was not, however, significantly better than detrended kriging for temperature, or better than ordinary kriging, co-kriging, nearest neighbour, and inverse distance squared for precipitation. Nevertheless, GIDS is considered preferable for the intended study because it is simple to apply while providing robust performance and low errors for both temperature and precipitation. Although specific forms of kriging (detrended kriging for *T* and co-kriging for *P*) have been shown to provide comparable performance, these kriging methods are ruled out because: 1) they are not as objective as GIDS: predictions depend on subjectively choosing the variogram model and the neighbourhood, 2) fitting variogram models is very time consuming, 3) the mathematics are complicated which means the results can be difficult to check and interpret, and 4) the kriging errors presented here are probably optimistic, since the cross validation was not truly independent of the input data.

GIDS provides cross validation errors comparable with those from other climate interpolation studies. Detrended kriging of monthly temperature in northern Minnesota gives a MSE of 0.734 $°C^2$ (Holdaway, 1996) which is higher than the GIDS MSE of 0.44 $°C^2$ from this study. An optimum combination of multiple regression and thin plate splines for interpolation of T in Great Britain achieves an r^2 (actual versus predicted) between 0.89 and 0.94 (Lennon and Turner, 1995): the comparable r^2 from the WCCBF data were between 0.83 and 0.96. Hulme et al. (1995) used a mixed spline-regression model to interpolate climate for "greater Europe" and give MAE's between 0.5 and 0.8 °C for January and July T_{max} and T_{min}, which brackets GIDS MAE's for January and July T_{mean} of 0.7 and 0.4 °C. The same study also found MAE's for January and July P (expressed as percentage of means) were 11.9 and 9.1 % which are remarkably close to the values of 11.1 and 8.1% respectively obtained using GIDS. In a comparison of methods for estimating annual precipitation in the central United States, universal kriging gave the lowest MAE of 0.96 inches (24.3 mm) (Tabios III and Salas, 1985). In comparison, GIDS was run for annual precipitation in the study region and obtained a very similar MAE (26.8 mm). Because of the sparse network of climate stations across the WCCBF, it was expected that errors would be substantially greater than for other regions, but in fact they appear very similar to other studies.

Given the low errors and robust performance, it is believed that GIDS can be successfully applied in other regions. It has already been used at the national scale to generate gridded climate for Canada (Price et al., 1998). There is potential for reducing GIDS errors further by including additional explanatory variables in the regression (as per Lennon and Turner, 1995). In the WCCBF region, however, any improvements would likely be small compared to the errors presented in this study and it was decided not to pursue this. Log-transforms of precipitation may also be beneficial in other regions, although they proved not to be warranted in the WCCBF. It should also be noted that GIDS cross validation errors were based on a planar X-Y co-ordinate system, but GIDS can just as easily use latitude and longitude. Although X-Y gave slightly lower errors than latitude-longitude, possibly because of the nonlinearity inherent in longitude at high latitudes; this may not be the case in other regions.

Other techniques

The method of thin plate splines is becoming popular for climate interpolation, and may have application in the WCCBF. It is doubtful, however, that splines would give lower errors since previous comparisons show that other methods, particularly kriging, can perform as well or better. In a comparison of two sets of data, Laslett (1994) concluded that "kriging sometimes outperforms splines by a considerable margin, and it never performs worse than splines." Hutchinson and Gessler (1994) re-analysed the data of Dubrule (1984) and concluded that Dubrule's kriging analysis had essentially the same predictive error as their optimum spline analysis. Lennon and Turner (1995) found that splines and regression performed equally when based on the same number of variables. Given the lack of evidence for superiority of splines[3], GIDS is particularly attractive because it is intuitive and relatively easy to grasp. It is also robust and simple to apply which suggests it may be useful as a benchmark for evaluating other techniques.

Applying GIDS

What accuracy will the GIDS method provide when interpolating to actual forest stands? This can never be answered quantitatively, since it would require long-term climate data for each stand, but some general conclusions can be drawn. On one hand, errors may be higher than presented here because these interpolations were tested against climate stations where conditions are fairly uniform (open, level ground, and frequently at airports), while the variations in topography and forest structure will probably lead to greater variability. On the other hand, errors will tend to be lower for two reasons. First, interpolation distances from the nearest climate station are generally shorter which should decrease errors. For example, the average distance from each cross validation test station to the nearest climate station was 91 km, but the average distance from each of the 121 stands to the nearest climate station is only 56 km. Second, the peripheral effect tends to give larger errors near the edge of the study region (Phillips et al., 1992). In this study, about half of the climate stations were on the periphery, but none of the 121 stands are peripheral, therefore interpolation to these stands should give better results. On balance it is likely that predictions for the stands of interest will have less error than those listed in Table 3-1 and Figure 3-4. It must be emphasized, however, that this statement applies to meso-climate, which may not be well correlated with the micro-climate at a specific site.

The strong seasonal trends in errors in this region must be considered in tree growth modelling. Temperature errors, and in fact variations across the region, are relatively small from May to October which brackets the growing season. During this period, absolute interpolation errors are likely to average about 0.4 °C. Errors in winter, however, are likely to be nearly double. Whilst this may be immaterial for tree growth, since trees are not photosynthesising at this time, it is important for determining soil temperature (Bonan, 1989) and the length of the growing season (Burton and Cumming, 1995; Sykes and Prentice, 1995), as well as the survival range of a species. In contrast to temperature errors, precipitation errors are low in winter and much higher in summer. Both are important for growth: summer precipitation limits moisture deficits while winter precipitation (snow) provides a moisture reservoir and affects soil temperature because of its insulating properties. Clearly, it is important to assess potential errors in all months. Error estimates from this study will be useful in defining limits for sensitivity testing of tree growth models.

Conclusion

A simple and effective method, termed GIDS, has been demonstrated for spatial interpolation of climatic Normals across the western Canadian continental boreal forest. This method provides cross validation accuracies at least as good as established kriging techniques without the complexity and subjectivity of kriging. The technique should also be applicable in other areas, although this would need to be tested, and may have potential for interpolation at increased temporal resolution. The GIDS method has been chosen to generate climatic data for 121 stands in the WCCBF to investigate long-term forest floor dynamics.

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[3] Subsequent to preparation of this chapter, a comparison of GIDS and a thin plate spline technique called ANUSPLIN showed ANUSPLIN provided lower errors in significantly more months than GIDS (Price, D.T., McKenney, D.W., Nalder, I.A., Hutchinson, M.F. and Kesteven, J.L., 2000. A comparison of two statistical methods for spatial interpolation of Canadian monthly mean climate data. Agric. For. Meteorol., 101: 81-94.)

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Tables

Table 3-1. *T* and *P* anisotropy data. AR=anisotropy ratio. θ = direction of major variance. Subscripts denote *T* or *P* data.

	AR_T	AR_P	θ_T	θ_P
Jan	5.9	1.7	22.5	22.5
Feb	5.9	2.3	22.5	22.5
Mar	6.1	5.4	22.5	22.5
Apr	8.1	1.8	45.0	135.0
May	10.5	4.2	45.0	0.0
Jun	9.7	4.2	45.0	0.0
Jul	2.8	3.6	45.0	0.0
Aug	2.1	2.3	45.0	45.0
Sep	6.4	1.7	22.5	67.5
Oct	6.1	3.8	22.5	67.5
Nov	6.3	3.7	22.5	45.0
Dec	6.1	2.3	22.5	22.5

Table 3-2. Cross validation errors averaged across all test sites and months for the seven interpolation methods (OK=Ordinary kriging; CK=co-kriging; DK=detrended kriging; UK=universal kriging; NN=nearest neighbour; IDS=inverse distance squared; GIDS=gradient plus inverse distance squared). Lowest error values in each row are in bold.

	1-OK	2-CK	3-DK	4-UK	5-NN	6-IDS	7-GIDS
Temperature errors (°C)							
ME	-0.19	-0.13	**0.03**	0.09	-0.18	-0.39	-0.06
MAE	1.14	0.79	0.54	0.89	0.75	0.87	**0.51**
RMSE	2.27	1.21	0.72	1.44	0.98	1.25	**0.66**
Precipitation errors (mm)							
ME	0.16	0.10	0.23	**0.03**	0.17	-0.23	-0.28
MAE	3.89	3.62	4.27	4.96	3.69	3.67	**3.59**
RMSE	5.92	5.00	5.84	10.47	5.15	4.96	**4.93**

Figures

Figure 3-1. Western Canada showing study region and climate stations.

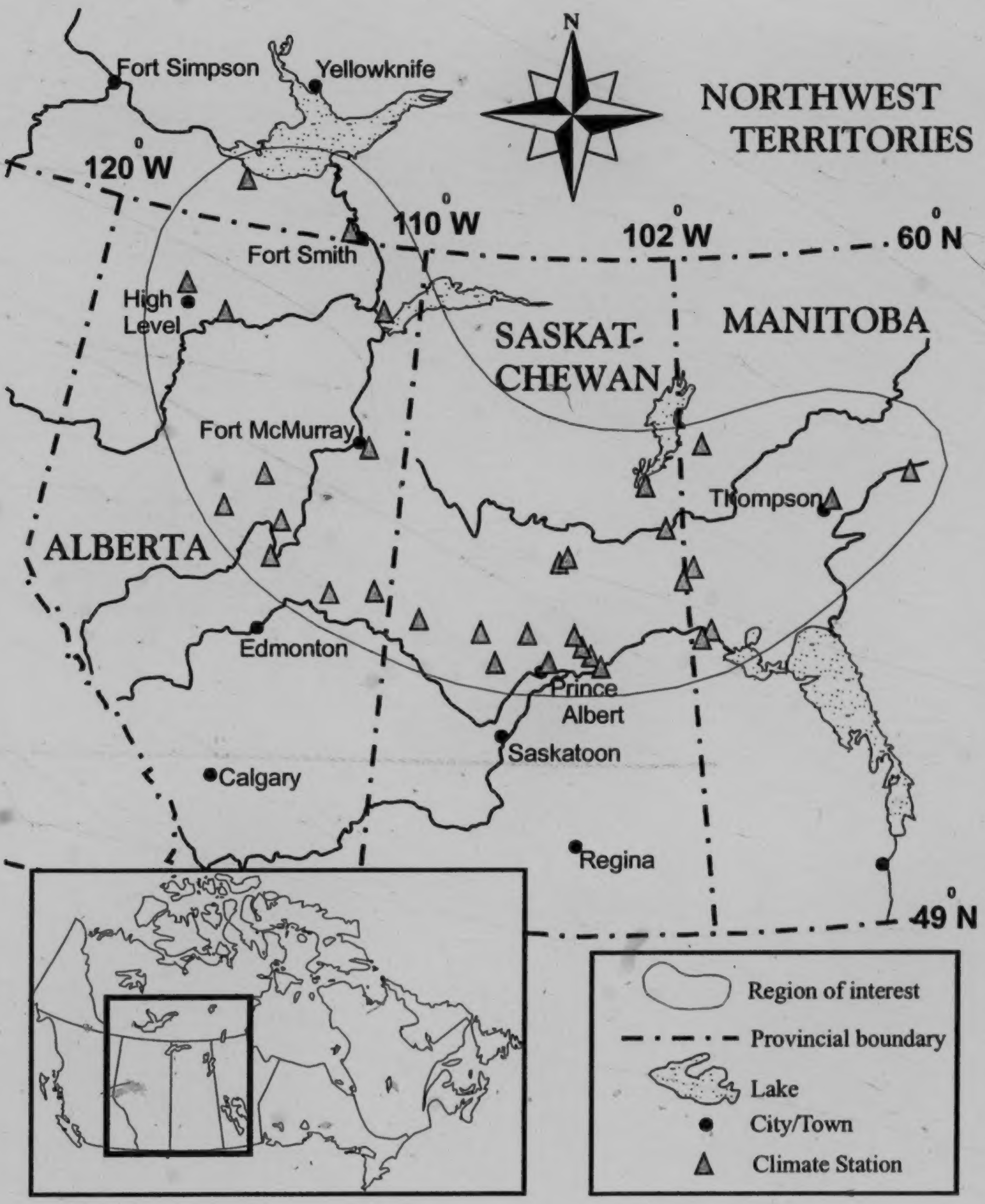

Fort Simpson
Yellowknife
N
NORTHWEST TERRITORIES
120° W
110° W
102° W
60° N
Fort Smith
High Level
SASKAT-CHEWAN
MANITOBA
Fort McMurray
Thompson
ALBERTA
Edmonton
Prince Albert
Saskatoon
Calgary
Regina
49° N
Region of interest
Provincial boundary
Lake
City/Town
Climate Station

Figure 3-2. Monthly temperature and precipitation variogram models used for ordinary and universal kriging (for clarity, only alternate months are shown).

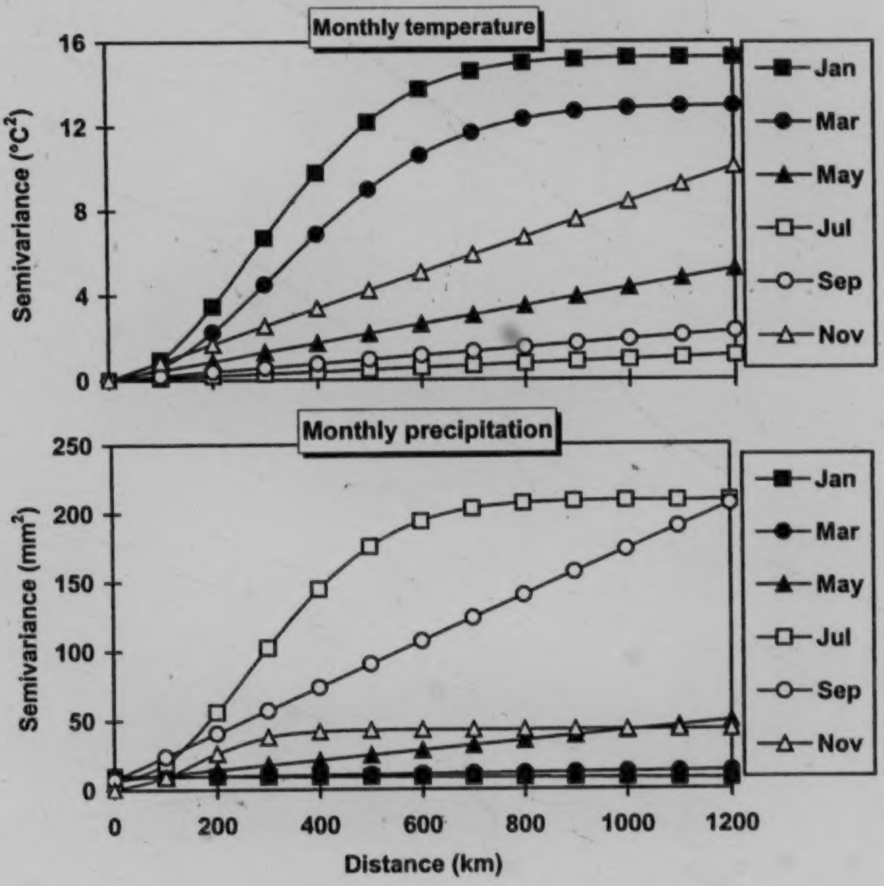


Figure 3-3. Coefficients and r^2 values from a multiple, linear regression of monthly temperature and precipitation against X, Y and elevation.

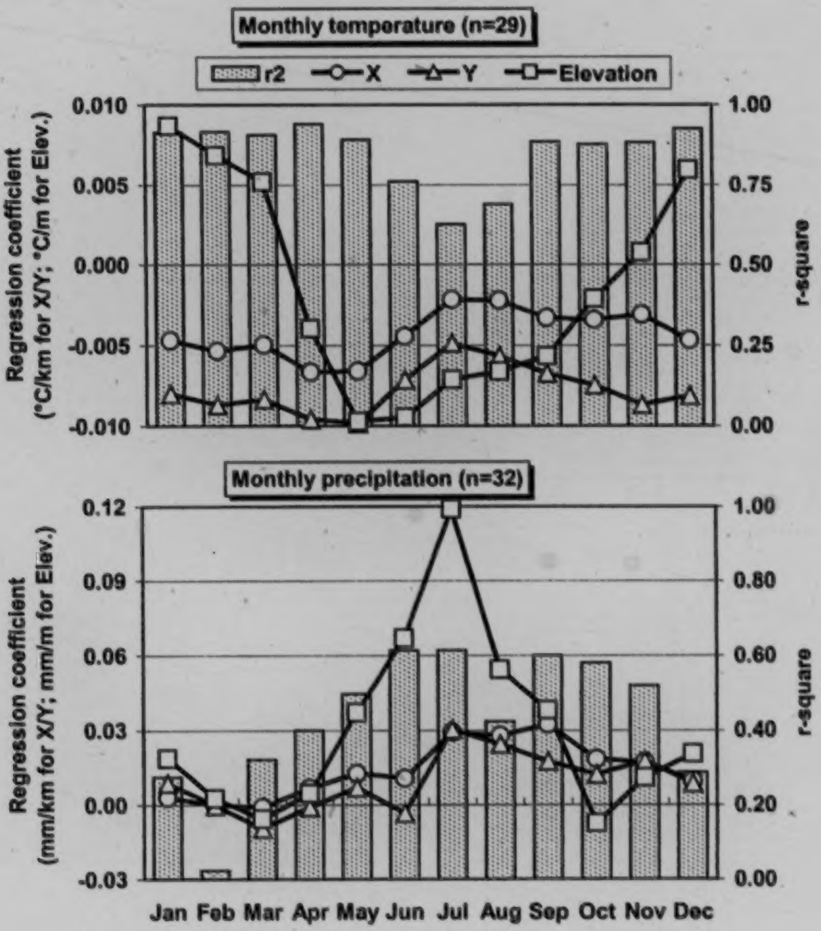
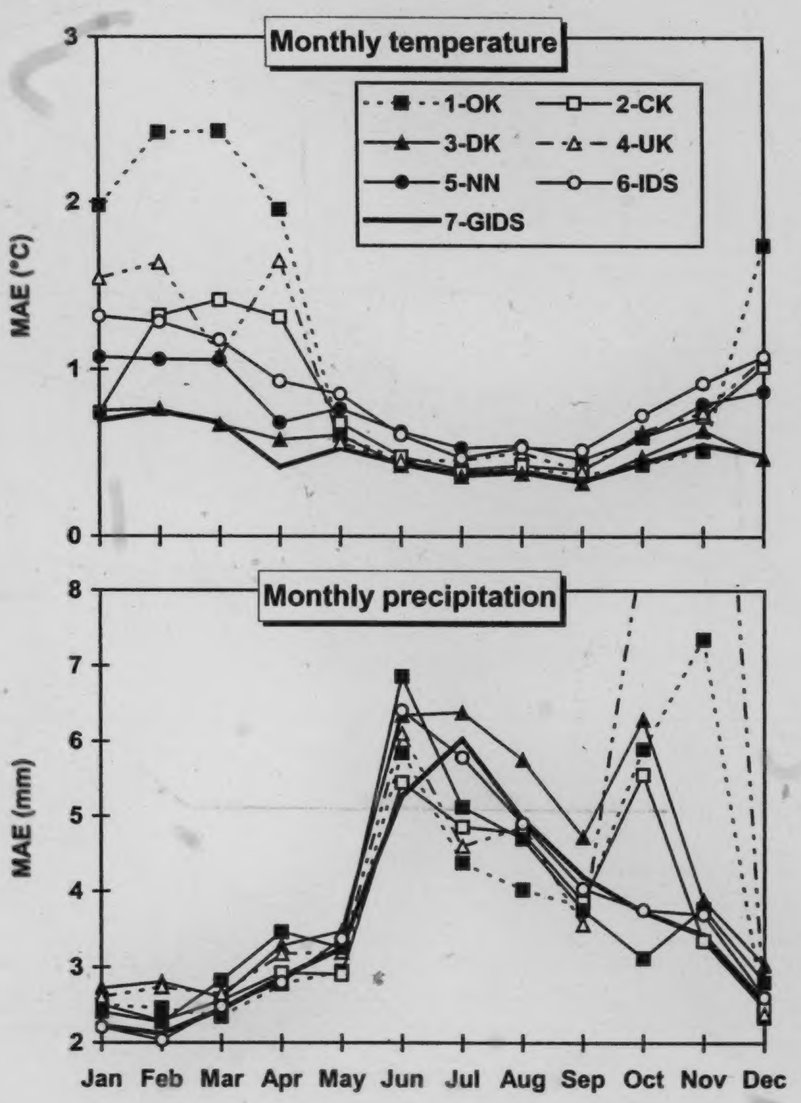


Figure 3-4. Cross validation MAE for mean monthly temperature and precipitation averaged across all test sites for seven interpolation methods. See Table 3-2 for abbreviations.



References

Ashraf, M., Loftis, J.C. and Hubbard, K.G., 1997. Application of geostatistics to evaluate partial weather station networks. Agric. For. Meteorol., 84: 225-271.

Bilonik, R.A., 1983. Risk qualified maps of hydrogen ion concentration for the New York state area for 1966-1978. Atmos. Envir., 17: 2513-2524.

Bonan, G.B., 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecol. Modelling, 45: 275-306.

Bradley, P., Gaston, G., Kolchugina, T. and Vinson, T.S., 1995. Simulating carbon storage in forests of eastern Russia. Water, Air, Soil Pollut., 82: 299-308.

Bugmann, H. and Fischlin, A., 1996. Simulating forest dynamics in a complex topography using gridded climatic data. Clim. Change, 34(2): 201-211.

Burton, P.J. and Cumming, S.G., 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water, Air, Soil Pollut., 82: 401-414.

Cressie, N.A.C., 1985. Fitting variogram models by weighted least squares. Math. Geol., 17: 563-586.

Cressie, N.A.C., 1986. Kriging nonstationary data. J. Am. Stat. Assoc., 81(395): 625-634.

Cressie, N.A.C., 1991. Statistics for Spatial Data. John Wiley & Sons Inc., New York, 900 pp.

Daly, C., 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteorol., 33: 140-158.

Dodson, R. and Marks, D., 1997. Daily air temperature interpolated at high spatial resolution over a large mountainous region. Clim. Res., 8(1): 1-20.

Dubrule, O., 1984. Comparing splines with kriging. Comput. GeoSci., 10: 327-338.

Eischeid, J.K., Baker, F.B., Karl, T.R. and Diaz, H.F., 1995. The quality control of long-term climatological data using objective data analysis. J. Appl. Meteorol., 34: 2787-2795.

Environment Canada, 1994. Canadian Monthly Climate Data and 1961-1990 Normals on CD-ROM, Version 3.0E. Environment Canada, Ottawa, Canada.

Halsey, L.A., Vitt, D.H. and Zoltai, S.C., 1995. Disequilibrium response of permafrost in boreal continental western Canada to climate change. Clim. Change, 30: 57-73.

Hammond, T. and Yarie, J., 1996. Spatial prediction of climatic state factor regions in Alaska. Ecosci., 3(4): 490-501.

Hogg, T.H., 1994. Climate and the southern limit of the western Canadian boreal forest. Can. J. For. Res., 24: 1835-1845.

Holdaway, M.R., 1996. Spatial modeling and interpolation of monthly temperature using kriging. Clim. Res., 6: 215-225.

Hulme, M., Conway, D., Jones, P.D., Jiang, T., Barrow, E.M. and Turney, C., 1995. Construction of a 1961-1990 European climatology for climate change modelling and impact applications. Int. J. Climatol., 15: 1333-1363.

Hutchinson, M.F. and Gessler, P.E., 1994. Splines -- more than just a smooth interpolator. Geoderma, 62: 45-67.

Journel, A.G. and Huijbregts, C.J., 1978. Mining Geostatistics. Academic Press, London, UK, 600 pp.

Kitanidis, P.K., 1997. Introduction to Geostatistics: Applications in hydrogeology. Cambridge University Press., Cambridge, 249 pp.

Laslett, G.M., 1994. Kriging Nonstationary Data. J. Am. Stat. Assoc., 89(426): 391-400.

Leemans, R. and Cramer, W.P., 1991. The IIASA Database for Mean Monthly Values of Temperature, Precipitation, and Cloudiness on a Global Terrestrial Grid. Working paper No. WP-90-41, Biosphere Dynamics Project. IIASA, Laxenburg, Austria.

Lennon, J.J. and Turner, J.R.G., 1995. Predicting the spatial distribution of climate: temperature in Great Britain. J. Animal Ecol., 64: 370-392.

Liski, J. and Westman, C.J., 1997. Carbon storage in forest soil of Finland: 1. Effect of thermocline. Biogeochem., 36: 239-260.

Longley, R.W., 1972. Climate of the Prairie Provinces. Climatological Studies Number 13. Environment Canada, Ottawa, Canada.

Longley, R.W. and Janz, B., 1978. The climatology of the Alberta Oil Sands Environmental Research Program study area. AOSERP Report 39. Fisheries and Environment Canada, Edmonton, Canada.

Nalder, I.A. and Wein, R.W., 1998. Spatial interpolation of climatic Normals: test of a new method in the Canadian boreal forest. Agric. For. Meteorol., 92(4): 211-225.

Nalder, I.A. and Merriam, H.G., 1995. Simulating carbon dynamics of the boreal forest in Pukaskwa National Park. Water, Air, Soil Pollut., 82: 283-298.

Olson, R., 1986. Climate of Wood Buffalo National Park. Environment Canada, Edmonton, Canada.

Pebesma, E.J., 1997. Gstat User's Manual. This is available from the URL http://www.frw.uva.nl/~pebesma/gstat/, 51 pp.

Pebesma, E.J. and Wesseling, C.G., 1998. GSTAT: A program for geostatistical modelling, prediction and simulation. Computers & Geosciences, 24(1): 17-31.

Peng, C., Apps, M.J., Price, D.T., Nalder, I.A. and Halliwell, D., 1998. Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada: 1. Model Testing. Biogeochem., 12(2): 381-392.

Phillips, D.L., Dolph, J. and Marks, D., 1992. A comparison of geostatistical procedures for spatial analysis of precipitation in mountainous terrain. Agric. For. Meteorol., 58: 119-141.

Price, D.T., Nalder, I.A. and Siltanen, R.M., 1998. A 10-km national climate surface for Canadian global change studies. In: Scaling and Modelling in Forestry: Applications in Remote Sensing and GIS, Proceedings of an International Workshop, 19-21 March 1988. Université de Montréal, Montréal, Canada., pp. 161-168.

Running, S.W., Nemani, R.R. and Hungerford, R.D., 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. Can. J. For. Res., 17: 472-483.

Stewart, R.B. and Cadou, C.F., 1981. Spatial estimates of temperature and precipitation normals for the Canadian Great Plains. Research Branch, Agriculture Canada, Ottawa, Canada.

Sykes, M.T. and Prentice, I.C., 1995. Boreal forest futures: modelling the controls on tree species range limits and transient responses to climate change. Water, Air, Soil Pollut., 82: 401-414.

Tabios III, G.Q. and Salas, J.D., 1985. A comparative analysis of techniques for spatial interpolation of precipitation. Water Resour. Bull., 21(3): 365-380.

Talkkari, A. and Hypén, H., 1996. Development and assessment of a gap-type model to predict the effects of climate change on forests based on spatial forest data. For. Ecol. Man., 83: 217-228.

Ver Hoef, J.M., 1993. Universal kriging for ecological data. In: Goodchild, M.F., Parks, B.O. and Steyaert, L.T., (Editors). Environmental Modeling with GIS. Oxford University Press, New York, pp. 447-453.

Webster, R. and Oliver, M.A., 1992. Sample adequately to estimate variograms of soil properties. J. Soil Sci., 43: 177-192.

4. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada[4]

Introduction

Boreal forests store approximately 800 Gt of carbon (Apps et al., 1993), an amount so large that small changes in fluxes can potentially have significant climate impacts. For instance, Kasischke et al. (1995) estimate that boreal forests could release up to 0.8 GtC yr^{-1} over the next 50 to 100 years, which would represent a 25% increase in the current buildup rate of atmospheric carbon and consequently could be a strong positive feedback on global climate change. The need to infer a 1.3 GtC sink to balance the global carbon budget (Schimel et al., 1996) in conjunction with indications of a substantial carbon uptake in northern terrestrial regions (Ciais et al., 1995; Francey et al., 1995; Keeling et al., 1996; Randerson et al., 1997), suggests that boreal forests may have been an important sink in recent years, but our understanding of the dynamics is not yet sufficient to identify the processes responsible or to predict future changes with any confidence.

Aboveground carbon pools and dynamics tend to be well characterized from forestry inventory data or stratified sampling (Botkin and Simpson, 1990; Kolchugina and Vinson, 1993a; Isaev et al., 1995; Kauppi et al., 1995; Kurz et al., 1995; Halliwell and Apps, 1997a; Kauppi et al., 1997; Price et al., 1997) but less is known about soil carbon. Although considerable data has been acquired at various scales (e.g. Post et al., 1982; Zinke et al., 1986; Halliwell and Apps, 1997b; Kauppi et al., 1997; Liski and Westman, 1997b; Liski and Westman, 1997a; Siltanen et al., 1997; Tarnocai, 1998), data on soil C dynamics in the boreal zone are limited and mostly concerned with the mineral soil changes over centuries or millenia (Protz et al., 1984; Protz et al., 1988; Harden et al., 1992; Liski et al., 1998). Few data exist for the dynamics of the soil organic layer, which is the focus of this study. This layer, termed the forest floor, comprises the L, F and H layers above mineral soil (Agriculture Canada Expert Committee on Soil Survey, 1987; Kimmins, 1987). It is not only significant as a carbon pool, accounting for as much as one half of soil carbon storage in non-peatlands (Huang and Schoenau, 1996), but is also important for forest fire fuel loads (Van Wagner, 1983; Forestry Canada Fire Danger Group, 1992) and for its role in regulating soil microclimate (Bonan and Shugart, 1989).

In Canada, the boreal forest can be divided into the Boreal East Ecoclimatic Province and the much drier Boreal West Ecoclimatic Province (Ecoregions Working Group of Canada, 1989; Siltanen et al., 1997), which will be referred to as the eastern boreal and western boreal, respectively. This study focuses on the western boreal. Here fire has historically been the principal disturbance agent with typical fire recurrence intervals of 50-100 years (Van Wagner, 1978; Johnson, 1981; Viereck, 1983; Murphy, 1985; Heathcott and Cornelsen, 1994; Larsen and MacDonald, 1995). The forest floor may be wholly or partially consumed by these fires, after which it rebuilds at a rate dependent on the balance between the rates of litter input and decomposition. Under a climate change scenario, it is likely that changes to this balance, as well as fire return intervals, will modify the amount of C stored in the forest floor across the landscape. Consequently, it is important to be able to predict this dynamic over timescales of decades to centuries to properly assess C budgets in the boreal forest.

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[4] A version of this chapter has been published. Nalder and Wein 1999. Global Biogeochemical Cycles. 13(4): 951-968.

Due to the lack of data, however, it is unclear how forest floors develop over the life of stands and how this dynamic is affected by climate and species. Long-term decomposition studies are showing that decay is asymptotic, implying a recalcitrant fraction (Berg et al., 1995), which leads to a hypothesis of long-term increases in the forest floor. The effect of climate is complex, since it affects not only decomposition rates but also productivity and hence the litter input to the forest floor. As a working hypothesis, it is proposed that decomposition rates exert more control, and that climates that are more limiting to decomposition will give greater forest floor accumulation. In upland areas of the western boreal, it is expected that colder and drier areas will be more limiting. To examine these hypotheses, this study examines two important but contrasting species, the coniferous *Pinus banksiana* Lamb. (jack pine) and the deciduous *Populus tremuloides* Michx. (trembling aspen). These species account for 20% and 29%, respectively, of the volume of timber in the western boreal (calculated from data in Gray, 1995) and dominate upland areas. Forest floor accumulation is expected to be less for *P. banksiana* than for *P. tremuloides* because litterfall from *P. banksiana* tends to be less (Gower et al., 1997) and the recalcitrant fraction of litter for boreal conifers can be much smaller than for deciduous species (Berg and Ekbohm, 1991).

The objective of this study is to measure the amount of organic carbon in the forest floor and aboveground vegetation and to relate forest floor carbon to stand age, species and climatic zone. Potential effects of vegetation components that contribute litter to the forest floor, and mineral soil characteristics which may affect site productivity and hence litterfall, will also be tested. Assessment of carbon pools and relating forest floor carbon to site conditions is essential for developing and validating process-based models which are needed to develop carbon budgets under climate change scenarios.

Methods

General

Upland forest stands were sampled in three distinct climatic zones of the western boreal. The three zones (Figure 4-1), together with the forest section designations of Rowe (1972), were: 1) central Saskatchewan (Mixed Wood), 2) northern Alberta/southern Northwest Territories (Hay River and Upper Mackenzie), 3) central Manitoba (Manitoba Lowlands and Nelson River). Sampling took place during the summers of 1995 to 1997. Suitable stands were chosen by visual inspection aided by pre-selection from forest inventory maps where available. Most stands were close to roads for ease of access. The approximate centre of each stand was identified, its latitude and longitude measured with a GPS receiver, and the elevation was determined from 1:50,000 topographical maps. To facilitate sampling, a 75 m transect was run in a random direction through the centre of the stand.

Stand selection

Within each climatic zone, stands of various ages (time since stand-replacing fire) that were dominated by *P. banksiana* or *P. tremuloides* were sampled. Because this study was interested in long-term dynamics, sampling was restricted to stands older than 10 years. This provided confidence that stands met criteria such as stocking and species dominance while avoiding what was expected to be a period of high variability during stand establishment. From a practical viewpoint, the high fire years of the early 1980's provided an ample selection of stands to begin the chronosequences, so that the minimum stand age was 14 years. For each zone and species, a chronosequence was developed of at least 10 stands, each generally larger than 4 ha, with as wide a range of ages as was available in the zone. Stands were even-aged and usually showed several types of evidence confirming their origin from a single stand-replacing fire. Stands were rejected if there was any indication of a fire subsequent to stand initiation, because any such fires may have removed a significant fraction of the forest floor. Sampled stands were clearly dominated by the selected species, with an objective of at least 90% dominance on a live tree biomass basis. Mixed stands are more common in the western boreal, but sampling these stands would tend to confound the effect of species. It has also been observed that forest floor depths in mixed stands are intermediate between those of *P. banksiana* and *P. tremuloides*, therefore by concentrating on stands dominated by one or the other species, it was expected to define the limits of forest floor accumulation. To minimize uncontrolled variability within each chronosequence, three further constraints were imposed on stand selection. First, stands were selected that had no obvious limitations to productivity, other than that imposed by regional climate and soil type. Second, to avoid the influence of runoff or seepage on moisture regime, stands in topographic depressions, toes and lower slopes were rejected as well as any stands that showed evidence of moisture input from ground water. Third, stands on steep slopes (greater than 30 degrees) were avoided to minimize differences in radiation exposure and thus micro-climate. Beyond these criteria, no attempt was made to control for factors such as parent material, texture, or soil order. Stands were sampled after leaf out and before leaf fall.

Forest floor carbon

For the purposes of this study, forest floor carbon (FFC) is defined as the amount of organic carbon per unit area above mineral soil that has accumulated since the last stand-replacing fire. This includes litter, ferment and humus materials, roots less than 1 cm diameter, fungal hyphae and other microbial biomass, but excludes partially decomposed coarse woody debris (rotten logs) which for reasons described later are treated separately. In each stand, 10 cores were taken at 5 m intervals along the sampling transect starting from the 10 m point. Cores were taken vertically through the forest floor and 15-20 cm into mineral soil using a specially designed corer with an internal diameter of about 5 cm (Nalder and Wein, 1998a). When cores could not be taken at the designated spot because of logs, large roots or rocks, the corer was moved 50 cm further along the transect.

Cores were transferred from the coring device onto an examining tray for measurement of layer depths and segregation of the moss/lichen layer (if present), the forest floor layer, and a mineral soil sample (when required). Any live vegetation, apart from moss and lichen, was removed. Layers were separated with a knife by cutting in a plane perpendicular to the axis of the core. The moss/lichen was removed at the top of the litter layer, which was essentially at the base of the photosynthesising tissue. The base of the FFC layer was defined by the midpoint of the fire scar, which was normally present and was assumed to result from the previous stand-replacing fire, or at the mineral soil surface if no fire scar was discernible. Generally, fires scars were thin, horizontal bands of charcoal fragments sitting on top of mineral soil, indicating an intense stand-replacing fire that had removed nearly all of the forest floor. In cases where more than two cores showed thick fire scars or fire scars intermediate in the forest floor, the stand was rejected. Cores containing unusually large accumulations of organic matter, such as rotten logs or squirrel middens, were flagged for separate analysis.

The samples were air-dried and returned to the laboratory for later analysis. Due to constant shifting of the base camp, most samples were rapidly brought to air-dry moisture content using a microwave oven. To avoid charring samples, a procedure was developed of incrementally drying while estimating the moisture content at the end of each step based on the percent weight loss and stopping when predicted moisture was in the 5-10% range. Nevertheless, a slight loss of sample generally occurred. This loss was measured by oven-drying samples from seven stands, re-wetting to original moisture contents, then "air-drying" using the microwave technique followed by conventional oven-drying. Weight loss attributable to microwave drying was 0.9±0.7%. The linear relationship between true oven-dry weight and that achieved after microwave-drying was used to correct the weights of the remaining cores that were microwave-dried. The correction was small relative to the standard errors achievable in this study. The air-dry FFC samples were prepared by chopping any woody matter into small fragments then grinding with a meat grinder and/or mortar and pestle. When suitably homogenous, a subsample of approximately 5 g was taken, oven-dried to constant weight at 75 °C then ashed at 450 °C for 16 hours, i.e., organic matter determined by loss-on-ignition (LOI).

To develop a relationship between organic carbon and LOI data, 10 samples from each species and each zone were randomly selected and total carbon content was measured using a Carla-Erba NA1500C induction furnace and CNS analyzer. Using HCl pre-digestion, organic carbon content was measured on 20 of the samples to establish that mineral carbon content was insignificant, i.e., organic carbon could be equated with total carbon. Organic carbon was related to LOI using a general linear model (SPSS Inc., 1996), and this relationship was used to estimate organic carbon content of all samples from the LOI data.

Stand age

Stands were aged from fire history records when available, otherwise from increment cores and fire scars. A minimum of 10 trees were cored in the vicinity of the transect and the number of rings were counted on site. Usually the ring counts from the cored trees were tightly clustered, indicating an even-aged stand. Stand age was estimated from the upper asymptote of ring counts plus a correction factor of 3-6 years to account for the time taken for trees to grow to the coring height, generally 50 cm for *P. banksiana* and 130 cm for *P. tremuloides*. The correction was subjectively estimated for each stand based on site conditions, experience with estimating ages in stands of known age, as well as measuring the number of years to reach coring height from trees cut at the base. Fire scars on trees at stand boundaries were used as corroborating information.

Vegetation variables

To characterize tree cover, records were taken of the species, height and diameter at breast height (dbh) of all trees greater than 1.3 m in height in three or four fixed area plots. Triangular plots were laid on alternate sides of the sampling transect and ranged in area from 11 m^2 for stands with more than 50,000 stems ha^{-1} to 173 m^2 for stands with less than 5,000 stems ha^{-1}. Ground slopes were measured in each plot. Aboveground biomass of each live tree was calculated from height and dbh using standard allometric equations (Evert, 1985), and the total for each species was divided by plot area and cosine of the ground slope to obtain biomass per unit area, then converted to C density assuming the commonly used value of 50% C content (Grigal and Ohmann, 1992; Kurz et al., 1992; Kolchugina and Vinson, 1993b; Kauppi et al., 1995; Liski and Westman, 1995; Karjalainen, 1996). Reported values for tree C density are the total for all species. Species dominance was calculated as live tree biomass of the dominant species as a percentage of total live tree biomass.

The shrub layer was characterized by recording the species and basal diameter of each erect, woody stem that was at least 4 mm in diameter in two fixed area plots at either end of the transect. Shrub density was extremely variable therefore plot sizes were determined for each stand with the objective of providing standard errors that were within 50% of the mean. Plot sizes ranged from 6.3 m^2 in stands with dense and uniform shrub layers to 173 m^2 in stands with widely spaced clumps of shrubs. Trees less than 1.3 m in height were included in the shrub layer. Biomass was calculated from allometric equations for that species (Smith and Brand, 1983) or for a similar species if no data were available. Carbon density was calculated as for trees.

The ground vegetation layer was characterized in five 1 m^2 quadrats spaced along the transect by estimating percent cover of five categories: mosses, lichens, grasses, legumes, and lastly, dwarf shrubs and forbs. Values were averaged across the five plots. Biomass values for grasses, legumes and dwarf shrubs and forbs were calculated from allometric equations (Ohmann et al., 1981) with C density calculated as for trees. To determine the importance of moss *vis-à-vis* lichen, a "moss dominance index" (MDI) was defined as %Moss / (%Moss + %Lichen). This was set to zero where the moss/lichen layer was absent.

Carbon density of the moss/lichen layer was determined by oven-drying this layer from each forest floor core to constant weight at 75 °C and converting to organic C assuming organic carbon is 50% of oven-dry biomass.

Climatic variables

The three climatic zones were chosen to provide contrasting extremes of temperature and precipitation within the western boreal. Stands were selected within or close to the BOReal Ecosystem-Atmosphere Study (BOREAS) Southern Study Area (SSA) near Prince Albert, Saskatchewan (Zone 1), in Wood Buffalo National Park near Fort Smith (Zone 2), and near the BOREAS Northern Study Area (NSA) centred on Thompson, Manitoba (Zone 3), which represent warm-dry, cold-dry and cold-wet conditions respectively. The main climatic variables for Prince Albert, Fort Smith and Thompson are given in Table 4-1.

To better assess the influence of climates, including any gradients that occurred within each zone, mean monthly temperature and mean monthly precipitation were estimated for each stand by spatially interpolating from surrounding climate stations. For this purpose, the "Gradient-plus-Inverse Distance Squared" (GIDS) technique (Nalder and Wein, 1998b) was applied to 1951-1980 Normals (Environment Canada, 1982; Environment Canada, 1983); these Normals were selected because they were more representative of long-term means and provided more climate stations than other 30-year periods. Mean annual temperature (MAT) and annual precipitation (P) were calculated from monthly values.

Mineral soil variables

The depth of unconsolidated material at each forest floor sampling point was checked with a 1 m steel rod. Permafrost or frozen layers were not a problem in the sampled stands therefore depth to shallow bedrock was easily ascertained. In most stands, bedrock was at least 1 m below the soil surface; for depths less than 20 cm to bedrock or to an impervious horizon the stand was rejected. Near the transect midpoint, a soil pit was excavated and field determinations of soil texture were made. The dominant texture of the upper 20 cm of mineral soil was categorized into four classes as Coarse (S, LS), Moderately coarse/Medium (SL, L, SiL, Si), Moderately fine (SCL, CL, SiCL) and Fine (SC, SiC, C) (Brady, 1990). At fixed intervals along the sampling transect, mineral soil samples were taken to characterize water retention. The samples were taken from the bottom of the appropriate forest floor core, generally 10-15 cm below the mineral soil surface. Three samples per stand were taken in zones 1 and 3 and one per stand in zone 2. Gravimetric field capacity and wilting point were measured using a SoilMoisture Equipment Corp. pressure plate apparatus. Field capacity was measured at -0.01 MPa for coarse textures and -0.03 MPa for finer textures (Hausenbuiller, 1985). Wilting point was measured at -1.5 MPa. Available water holding capacity (AWC) was calculated as the difference between field capacity and wilting point. A portion of each mineral soil sample was checked for organic matter content by loss-on-ignition, and bulk density (*Db*) was estimated using the relationships developed by Grigal et al. (1989) following Halliwell et al. (1997b) and Siltanen et al. (1997).

Statistical analysis

For exploratory analysis, Pearson's correlation coefficients were calculated for all quantitative variables (SPSS Inc., 1996). Analysis of covariance was then carried out to examine the effect of species and zone (fixed factors) and stand age (covariate) on FFC (dependent) using a general linear model type III (SPSS Inc., 1996). Species-specific models using other independent variables were developed with stepwise multiple linear regression to determine the simplest model that explained the most variation with all terms significant (SPSS Inc., 1993). The level of significance for all tests was 5%. Levene homogeneity tests, normal probability residual plots, and plots of residuals versus predicted and independent variables were used to check for violations of the assumptions of ANOVA. To better meet these assumptions, FFC and stand age were natural log transformed and an arcsine square root transformation was applied to MDI.

Results

A total of 80 stands were sampled. The major variables for each stand are listed in Table 4-2.

LOI-Organic C relationship

Inorganic carbon content of forest floor samples was very small (0.4±0.2%, n=20) therefore total carbon data were used as a measure of organic carbon. Percent carbon was closely related to percent organic matter as determined by LOI (Figure 4-2). There was also an effect of the amount of organic matter and of climatic zone, but not of species (Table 4-3). The fitted model, which was used to estimate percent C from organic matter as determined by LOI, accounted for 94% of the variation in the data.

Carbon pools

Averaged over all stand ages in all climatic zones, trees were the major component of C storage in the sampled stands (Table 4-4). Forest floor carbon represented 24% and 33% of the stand totals for *P. banksiana* and *P. tremuloides*, respectively. Moss/lichen did not occur to any significant amount in *P. tremuloides*, but comprised 3.2% of the total in *P. banksiana*. Shrubs were a smaller component, comprising 0.6% and 1.8% of total C, respectively. For both species, ground vegetation was only 0.3% of the total.

Chronosequences

Of concern in a study of this type where many factors cannot be controlled is the comparability both within and between chronosequences (Pickett, 1989); results must be viewed in the context of the potential variability caused by these factors. Table 4-5 summarizes some important characteristics of each of the six chronosequences. Stand ages ranged from 14 to 149 years. Despite the susceptibility of old *P. tremuloides* trees to heart rot and the successional shift to mixed wood, the upper age limits of *P. tremuloides* sequences were higher than those of *P. banksiana*. This occurred because of the difficulty in finding *P. banksiana* stands that had not been subject to low-intensity post-establishment ground fires. Seventy of the 80 stands had greater than 90% dominance by the selected species; the remainder were judged to be acceptable because the apparent low purity resulted from large, but isolated, *Picea glauca* trees that fell within a tree sampling plot but were well off the transect. Based on interpolated values of mean annual temperature and precipitation, the stands clustered into three distinct climatic regimes, although the differences among zones is not quite as great as indicated by Table 4-1. Variations in soil characteristics were unavoidable, partly because different species thrive on different soils and partly because soil genesis processes were different in each zone. All *P. banksiana* stands were on coarse textured soils, either sand or loamy sand, whereas *P. tremuloides* stands were generally on finer soils and displayed textural differences between zones. The differences in texture between species are reflected in available water holding capacity, with *P. banksiana* stands having much lower values. The zonal differences in texture for *P. tremuloides*, however, are not evident in available water holding capacity values, perhaps because these values are also affected by organic matter content.

Tree C showed strong and linear increases with time (Figure 4-3). Tree C accumulation rates (growth rates) ranged from 47-98 gC m^{-2} yr^{-1}, being highest for *P. tremuloides* in all zones (Table 4-5). Zone 1 had the highest accumulation rates for both species, with little difference between zones 2 and 3. There was no evidence in any of the chronosequences of an upper asymptote, i.e., linear models were most appropriate in all cases.

Moss-plus-lichen C was only a significant component in *P. banksiana* stands, where strong, linear increases with time were observed (Figure 4-4). Accumulation rates were small in comparison to trees (2.5-2.7 gC m^{-2} yr^{-1}) and there was little difference among climatic zones (Table 4-5). In contrast, zones had differing degrees of moss dominance; zone 2 was moss-dominated while zone 3 was lichen-dominated.

In contrast to trees and moss/lichen, other components of stand vegetation showed no trend over time for any of the chronosequences. Mean values for shrubs ranged from 0.03-0.04 kgC m^{-2} for *P. banksiana* and 0.09-0.30 kgC m^{-2} for *P. tremuloides* (Table 4-5). For *P. banksiana* there was little difference among zones, but *P. tremuloides* in zone 3 had much higher values than either zone 1 or 2. Apart from *P. tremuloides* in zone 3, shrub layer C was small compared with trees. Dwarf shrub and forb C was remarkably consistent among chronosequences (Table 4-5), and was much less than shrubs, averaging 16 and 15 gC m^{-2} for *P. banksiana* and *P. tremuloides* respectively. Grasses were an even smaller component, averaging 3 and 10 gC m^{-2}, respectively. Legumes, which may alter nutrient dynamics due to their N-fixation, were found in nearly all stands, but were an extremely small component, averaging 0.1 and 1.4 gC m^{-2}, respectively.

Rotten log component

Rotten logs were encountered in 55 of the 800 cores, and on average had a C density 2.2 times that of cores that did not pass through rotten logs. This infrequent occurrence, combined with the high C density, gave a mean FFC coefficient of variation of 39% compared with 33% when rotten log cores were excluded. Separate treatment of the rotten log component was desirable, not only to minimize the variability of FFC, but also because it was believed that the dynamics of bole decay was very different to that of other litter. There were, however, insufficient rotten log cores to carry out a statistical analysis as for FFC, therefore only general trends are presented. By combining climatic zones and taking means across 20-year age classes, a pattern of rotten log dynamics can be ascertained (Figure 4-5). The means and standard errors across all ages of *P. banksiana* and *P. tremuloides* stands were 0.18±0.05 and 0.13±0.04 kgC m^{-2}, respectively.

Other unusually large cores occurred with squirrel middens, root bases of *Alnus crispa*, or small depressions filled with windblown litter. This was measured in 4 stands of the 80, and these cores were excluded from FFC calculations. Averaged across all stands, the excluded cores would add 30 gC m^{-2}, or 1.4%, to the overall FFC mean.

FFC dynamics

There was considerable variation in FFC but some general trends are apparent (Figure 4-6). FFC was significantly related to stand age, as well as to climatic zone and species as interaction terms with age (Table 4-6). All terms were highly significant and the model explained 73% of the variation in FFC. There was high correlation among many of the variables (Table 4-7), suggesting that other variables may help explain FFC variation. Since the species interaction term accounted for a large part of the variation, each species was separately examined to identify related variables for each. From the many regression models tested, the best in terms of explaining the most variation while having the minimum number of significant terms are given in Table 4-8. For *P. tremuloides*, stand age, MAT and *P* were highly significant and mineral soil bulk density was marginally significant. Figure 4-7 shows the relationships between FFC and age, MAT and *P*. The model explained 64% of the variation. For *P. banksiana*, the best model revealed that FFC was positively related to moss dominance index (Table 4-8), i.e., moss dominated stands tended to have the highest FFC values (Figure 4-8).

Discussion

General

Organic matter content, as determined by LOI, proved to be a good predictor for organic carbon content of the forest floor (Table 4-3). The van Bemmelen factor (58%) is often used (e.g. Paré and Bergeron, 1996; Halliwell and Apps, 1997b) but data presented here show that the appropriate conversion factor is affected not only by zone but also by the amount of organic matter in the forest floor. The values obtained here are generally lower than the 58% assumption, as well as being lower than the model of David (1988) for forest floors in Minnesota, Wisconsin and Michigan (as shown in Figure 4-2), which supports the need for study-specific values.

The definition of FFC used here excludes some components that would normally be part of the forest floor C pool. The largest, and most important to dynamics, is the component represented by rotten logs which has not been previously studied in boreal forests. Although data from this study are limited, it is sufficient to indicate the importance of this component for further study. On average, rotten log C density was 14% of FFC in *P. banksiana* stands and 5% in *P. tremuloides* stands and the dynamics were quite pronounced (Figure 4-5). The pattern is interpreted as a pulse of dead trees entering the forest floor many years after stand establishment, then slowly decaying over the next 60-80 years with a second pulse (in *P. tremuloides*) coming from stand break-up. The timing of the pulse is much later for *P. banksiana* than *P. tremuloides*, which accords with field observations. *P. tremuloides* snags fall about 5 years after fire, then lay flat on the ground where they soon enter the forest floor pool. In contrast, *P. banksiana* snags often don't fall for 10-20 years and can remain propped above ground for decades thereafter.

Other large concentrations of forest floor materials can occur due to squirrel middens, root balls of *A. crispa*, and small depressions such as burrows or holes left by tap roots that fill up with litter. Across all stands, these only contributed 29 gC m^{-2}, but added considerable variability to the data, which was the reason this component was excluded from the dynamics analysis. Charcoal and forest floor materials below the fire scar were also excluded, since this is not part of the accumulation since stand replacement. In practise there were few cores where there was any material apart from charcoal below the fire scar, probably because selected stands oiginated from severe fires that would have removed most or all of the forest floor. Stands subject to less severe fires could be expected to have higher total forest floor carbon densities. No data were obtained on the charcoal component but *Zackrisson et al.* (1996) measured 0.10-0.21 kgC m^{-2} in the forest floor of a chronosequence of *Pinus sylvestris* in northern Sweden with no significant change over time. This inert C would play little role in dynamics.

The selection of stands will also give forest floor values different to those that would be observed at the landscape scale. On one hand, the selection of "fully stocked" stands should mean greater litterfall and hence more forest floor C than would be observed at the landscape level. On the other hand, stands on lower slopes have been reported to accumulate more forest floor (Huang and Schoenau, 1996) therefore selected stands, which were on upper slopes, may underestimate landscape levels. Data presented here may also underestimate true accumulation rates because the possibility of undetected, post-establishment surface fires cannot be completely ruled out. Considering all these factors, it likely that the regression models will tend to underestimate actual forest floor C pools in upland stands of the two species studied here.

Species effects

FFC was strongly related to species (Figure 4-6, Table 4-6). The effect of species is not surprising: in the western boreal the differences between *P. banksiana* and *P. tremuloides* are generally obvious even to casual observation. In other areas, differences between these species are established (Alban, 1982; Grigal and Ohmann, 1992) as are differences among *P. tremuloides*, *Picea glauca* and *Betula papyrifera* (Paré and Bergeron, 1996) as well as between *Pinus sylvestris* and *Picea abies* (Liski and Westman, 1997a).

FFC values estimated from the ANCOVA model (Table 4-6, Figure 4-6) are in line with values observed in other studies. In 50 and 60-year old upland *P. tremuloides* stands near Fairbanks, Alaska, forest floor biomass is 4.75 kg m^{-2} (van Cleve et al., 1983), or 2.8 kgC m^{-2} assuming 58% C content, which is very close to model estimates of 2.7-2.9 kgC m^{-2} for the same ages in zone 2 (zone 2 has a comparable MAT and *P* to Fairbanks). At the BOREAS SSA, the upper slope forest floor in an 80-year old *P. tremuloides* stand averages 4.1 kgC m^{-2} (Huang and Schoenau, 1996) which is 35% higher than model estimates for zone 1. There is considerable local variation, however, because in mature *P. tremuloides* in the same area *Gower et al.* (1997) report a forest floor of 1.94 kgC m^{-2}. Across the BOREAS SSA and NSA, forest floor C densities for stands dominated by *P. banksiana* and *P. tremuloides* are 1.32±0.20 and 2.83±0.41 kgC m^{-2}, respectively (mean±SE calculated from data in Halliwell and Apps (1997b)), which are close to model estimates of 1.23 and 2.69 kgC m^{-2}, which are the means of zone 1 and zone 3 assuming an average age of 75 years. Across the western boreal, forest floor C densities are 1.78±0.13 and 2.35±0.11 kgC m^{-2}, respectively (mean±SE calculated from the Canadian soil C database of Siltanen et al. (1997)). These means are 37% higher and 17% lower than model estimates for *P. banksiana* and *P. tremuloides*, respectively, when averaged across the three zones and assuming an average age of 75 years. These differences are possibly due to the inclusion of mixed stands in the soil C database; mixed stands in upland areas of the western boreal tend to give forest floor accumulations that are intermediate between those of *P. banksiana* and *P. tremuloides*. By contrast, a pure 62-year old *P. banksiana* stand in the eastern boreal (northern Ontario) has a forest floor C density of 2.03 kgC m^{-2} (Morrison et al., 1993) which is considerably higher than model estimates for either zone 1, 2 or 3 at this age. This is likely due to regional differences, possibly climatic, because *P. banksiana* forest floor C density is 68% higher across the eastern boreal than the western boreal (data from Siltanen et al. (1997)).

Stand Age

The positive and highly significant relationship between FFC and stand age (Table 4-6) indicates that C continues to increase in the forest floor over the life of a stand. There was, however, a strong interactive effect of species. When separate regressions were carried out for each species, age was highly significant for *P. tremuloides* but not for *P. banksiana* (Table 4-8). These statistical tests must be viewed in the context of the assumption that independent variables are accurately known. For the majority of stands, year-of-origin could not be established with certainty because fire history records did not exist. The process of ageing from increment cores and fire scars is subject to several potential sources of error (Johnson and Gutsell, 1994), and although it is not possible to provide any objective measure of these errors, it is expected that they would have a coefficient of variation of about 2% of the estimated age. Regression statistics, however, are robust with respect to moderate violations of assumptions (Zar, 1984), which along with the high levels of significance obtained for *P. tremuloides*, provides confidence that the hypothesis of long-term forest floor accumulations is supported for this species.

With other species, there are strong indicators of long-term forest floor or humus accumulation (Heinselman, 1973; Bradshaw and Zackrisson, 1990; Gorshkov et al., 1996; Wardle et al., 1997) but comparative data are limited for *P. tremuloides*. A similar increase to that found here has been reported for a chronosequence in Minnesota (Stoeckeler, 1961). Another Minnesota study found that age was a significant factor in a combined model (Grigal and Ohmann, 1992), although this may have been due to effects of other species because *P. tremuloides* was only one of five forest types in this model. A strong and significant increase of the FH layer was found over a 47-231 year chronosequence in Quebec (Paré et al., 1993), although in a shorter chronosequence (29-123 years) age was not a significant factor (Paré and Bergeron, 1996). In central Alaska, Van Cleve and Noonan (1975) suggest that *P. tremuloides* forest floors are at or approaching steady state by 120 years, which implies an age dependence for at least this period. Results from this study provide valuable support for the above evidence of long-term forest floor accumulations in *P. tremuloides* stands.

There was no support for long-term forest floor accumulations for *P. banksiana*. Data from the literature are inconclusive. Trumbore et al. (1997) report accumulations of 4-14 gC m^{-2} yr^{-1} at two jack pine study sites in the BOREAS NSA, but these data assume a linear increase from stand establishment and therefore do not discriminate between long-term and short-term increases; they also include live moss, which as noted here, was strongly related to age (Figure 4-4). In contrast, the forest floor is less in old jack pine sites than in young jack pine sites in both the NSA and SSA (Gower et al., 1997), suggesting a loss of C with age. In New Brunswick, MacLean and Wein (1977) found no evidence for increases in the forest floor of a 13-57 year chronosequence of pure *P. banksiana* stands, and forest floor increases have been reported to level off by the end of a 2-16 year chronosequence (Krause, 1998). However, Foster et al. (1995) found significant increases over about 20 years in the humus layer of two mature *P. banksiana* sites in Ontario, and at another Ontario site, forest floor C in a 62-year old *P. banksiana* stand was 2.03 kgC m^{-2} versus 1.56 kgC m^{-2} in the same stand 20 years earlier (Morrison et al., 1993), indicating long-term accumulations in mature stands. The accumulation rate in the latter instance (24 gC m^{-2} yr^{-1}) is substantial, and if similar rates applied in the western boreal, this study should have been able to detect this. Given that existing data on *P. banksiana* long-term forest floor dynamics are contradictory, the lack of an age effect from this study provides new evidence against long-term accumulations in *P. banksiana*.

Climate

Climate also had an effect on forest floor dynamics. In the combined ANCOVA model (Table 4-6), climatic zone was significant as an interaction term with stand age. This result, however, must be viewed in the context of a climate which has not been constant. The most pronounced trends have occurred for temperature. From 1861-1990, mean annual temperatures in the northern hemisphere increased by about 0.8 °C with decadal variations up to about ± 0.3 °C (Jones, 1994 Figure 4). Recent regional rates of change have been much greater: from 1961-1990, increases of about 0.5, 0.5 and 0.4 °C per decade occurred in zones 1, 2 and 3, respectively (Chapman and Walsh, 1993, Figure 1). Such increases are substantial relative to the 3.1 °C range in zonal MAT's in this study and have the potential to confound the zonal effect. This is considered unlikely, however, for two reasons. First, the differences between zones have been maintained, i.e., the changes in each zone have been of the same sign and very similar magnitude. Second, most of the warming has occurred since 1980 (Chapman and Walsh, 1993, Figure 3) which is a short period relative to timeframes of this study.

Most of the explained variation in the combined ANCOVA model was from the species interaction term. Such a strong effect may mask species-specific effects. Separate regressions for each species (Table 4-8) examined this, as well as the effect of quantitative climatic variables. These regressions revealed that no climatic variables significantly affected FFC for *P. banksiana*. For *P. tremuloides*, however, FFC was positively related to MAT and negatively related to *P*. Figure 4-9 illustrates these effects. Highest FFC occurs for MAT and *P* values corresponding to zone 1 with a 14% decrease for zone 2 and a 36% decrease for zone 3. It was expected that FFC would be highest in the climatic zone most limiting to decomposition, i.e., zone 2 which has low MAT and *P* values, but this did not occur. Zone 1 had the highest FFC and also the highest tree C accumulation rates (Table 4-5), which suggests that litter production may be a more important factor than decay in influencing FFC dynamics.

Climatic effects on forest floor thickness have been detected in Maine (Simmons et al., 1996) but comparative data for the boreal are limited. In a N-S transect of Finland, MAT had no effect on organic layer C (Liski and Westman, 1997a). For *P. tremuloides*, the forest floor is higher in the BOREAS SSA old aspen site than in the NSA old aspen site (Gower et al., 1997) which accords with findings here for the differences between zone 1 and zone 3. Age differences may be confounding, however, because the SSA site was 12 years older than the NSA site. Based on data from Halliwell and Apps (1997b), the mean organic horizon C density was significantly lower for the ten *P. tremuloides* sites within zone 1 than the seven sites within zone 3 (t-test, 0.01 significance level), which is the reverse of what was expected. This is difficult to explain, except to note that factors such as age, species dominance, stocking and slope position were not controlled in the Halliwell and Apps study and may be confounding. For *P. banksiana*, there was no evidence for climatic effect in data from this study or in the literature. On the BOREAS transect, the forest floor in the NSA old jack pine site is 21% lower than in the SSA site, but is 122% higher in the young jack pine sites (Gower et al., 1997) which suggests that factors other than climate are controlling. A comparison of means for *P. banksiana* sites in zones 1 and 3 using the data set of Halliwell and Apps (1997b), showed no significant difference. In view of the extremely limited information available on climatic effects within the boreal, this study provides valuable new data.

Moss Dominance

For *P. banksiana*, MDI was the only variable strongly related to FFC (Table 4-8, Figure 4-8). This was not unexpected because it had been observed that forest floors under continuous lichen cover were invariably thin while there were often substantial accumulations under continuous moss cover. Factors controlling moss dominance, however, are less clear. To investigate, a stepwise linear regression was carried out for *P. banksiana* stands using variables that were highly correlated with MDI (Table 4-7): MDI was positively related to tree C (Sig. = 0.001), positively related to dwarf shrubs and forbs C (Sig. = 0.001) and negatively related to *P* (Sig. = 0.01) ($r^2 = 0.65$). The relationship with tree C is probably due to reduced shading of the ground in stands with lower biomass: mosses are easily desiccated when exposed to sunlight (Tamm, 1964; Bonan and Korzuhin, 1989). Dwarf shrubs and forbs may be responding to the same factors, rather than being a control on moss dominance. The negative relationship with *P* is puzzling. It was expected that xeric sites would have proportionately less moss. It may be that textural differences among zones are confounding (all *P. banksiana* stands in zones 1 and 3 were on sand but half the stands in zone 2, which had the lowest *P*, were on finer textured loamy-sands), but the fact that water holding capacity variables were not significant suggests soil physical properties were not important. Clearly moss dominance is an important factor in predicting FFC for *P. banksiana*, but more research needs to be done to resolve its controls.

Soil Physical Properties

There was no significant relationship between mineral soil properties (bulk density, texture class, field capacity, wilting point, AWC) and FFC for *P. banksiana*. In contrast, bulk density was negatively related to FFC for *P. tremuloides* (Table 4-8) and texture class was also significant when substituted for bulk density in the model. However, water holding capacity variables were never significant, and bulk density and texture class were only marginally significant. Consequently it would be unwise to draw any conclusions about the effect of mineral soil properties, except to note that such an effect, if it exists, is small and therefore unlikely to be confounding the effect of zones.

Trees

Tree litter forms the major input to the forest floor. Not surprisingly tree C is highly correlated with FFC and stand age (Table 4-7) which raises the question of whether FFC in *P. tremuloides* stands is responding to age directly or indirectly through tree C. Tree C could be substituted for age in the regression with only a slight loss of explained variance and with high significance for the tree C term (Sig. < .001). This is consistent with the idea that the effect of age on FFC is mediated through age effects on tree growth and the litter input from trees into the forest floor.

It was surprising that patterns of tree C accumulation were linear, rather than the expected sigmoidal curve commonly used to describe forest growth. Sigmoidal curves, however, gave unrealistic fits for all chronosequences. The absence of a lower inflexion is likely due to stands younger than 14 years being excluded from the chronosequences. Polynomial and logarithmic forms that allowed reduced C accumulation in old stands were also tested, but linear models always gave higher significance. The lack of an upper asymptote is probably due to the slow C accumulation rates in the western boreal (Gower et al., 1997) which means that stands may not reach a maximum biomass over the age ranges sampled here, e.g., pine and hardwood Yield Curves for Alberta show no evidence of an upper asymptote in volume per hectare for at least 180 years (Alberta Forest Service, 1985). Second, the average standard error was 14% of the stand mean; with this variability, it would be difficult to detect a gradual tailing off in growth rates.

Understory vegetation

It was suspected that FFC would correlate with understory biomass, particularly in *P. tremuloides* stands, because the understory in this region can form much of the aboveground litter input to the forest floor. However, none of the understory components (shrubs, dwarf shrubs and forbs, legumes, grasses) was a significant factor in any of the regressions. The lack of significance for shrub C was particularly surprising, because shrubs were by far the largest component of the understory (Table 4-4). Admittedly shrub C was a small component relative to trees (0.9% and 2.7% for *P. banksiana* and *P. tremuloides*, respectively), but most C in trees is in stems, and stems, which eventually form rotten logs, are excluded from the definition of FFC. Consequently, shrubs can form a large fraction of leaf litter despite their relatively low biomass, e.g., in mature aspen in the BOREAS SSA, the understory forms only 0.8% of living vegetation, but contributes 21% of litter (from data in Gower et al., 1997) and shrubs have nearly twice the leaf area of the overstory *P. tremuloides* (Black et al., 1996). Even with a small biomass, shrubs have the potential to be a large contributor to the forest floor. Three explanations for their lack of significance in the regression can be suggested. First, the effect may exist but could not be discerned because of high variability in the shrub C estimates. Second, higher "quality" of shrub litter may lead to faster decomposition that tends to offset the shrub litter contribution. Third, stand-level leaf area may be constrained by site conditions so that any reduced productivity of trees, as may occur due to insect attack or windthrow, is counterbalanced by greater productivity of shrubs, i.e., shrubs are opportunistic.

Climate change implications

The forest floor was an important pool of C in the sampled stands. Excluding mineral soil and dead wood pools, which were not sampled, total C storage in *P. banksiana* and *P. tremuloides* stands was 5.6 and 8.5 kgC m^{-2}, respectively, with FFC accounting for 24% and 33% of these totals. Given that the definition of FFC probably underestimates actual forest floor C pools (see General section) and that *P. banksiana* and *P. tremuloides* account for nearly half of timber volume in the western boreal, it is concluded that the forest floor is an important pool of C in this region and therefore should be considered in climate change projections.

The regression models in Table 4-8 can provide limited guidance on the impacts of a changing climate because: (1) they are parameterized under a pattern of climate change that undoubtedly will be different in the future, (2) they are based on stands with very specific characteristics and therefore may be limited in spatial application, and (3) they cannot account for factors such as CO_2 fertilization and its impacts on litter quality. Nevertheless, they are useful to illustrate the potential for change. There are three main mechanisms by which a changing climate may alter forest floor C storage. First is the direct impact of MAT and *P* changes on FFC in *P. tremuloides*. For example, in zone 2 the Canadian General Circulation Model predicts equilibrium MAT and *P* increases of about 3°C and 20% respectively due to CO_2 doubling (Bergeron and Flannigan, 1995), which would result in values similar to present day zone 1. For a stand age of 75 years, the regression model indicates a 22% increase in FFC. Second, the age effect in *P. tremuloides* suggests that forest floor C storage will also be sensitive to disturbance intervals. Fire regimes in particular have historically been sensitive to climate (Clark, 1988; Bradshaw and Zackrisson, 1990; Clark, 1990; Bergeron and Flannigan, 1995; Larsen, 1997) and are expected to change considerably under climate change scenarios (see review in Weber and Flannigan, 1997). A reduction of the fire return interval from 75 to 50 years in zone 2 could potentially reduce mean *P. tremuloides* FFC by 12% (based on the regression model, a negative exponential cumulative fire interval distribution, and mean zonal values of MAT, *P* and bulk density). Third, shifts in the distribution of species have been hypothesized or predicted to occur as a result of climate change (Pastor and Post, 1988; Wein, 1990; Landhäusser and Wein, 1993; Hogg, 1994; Burton and Cumming, 1995; Thompson et al., 1998), and in western Canada, dramatic changes in the distribution of *P. banksiana* and *P. tremuloides* are predicted under a doubled CO_2 climate (Lenihan and Neilson, 1995). Given the effect of species reported here, replacement of *P. tremuloides* by *P. banksiana* could be expected to substantially reduce forest floor C (see Figure 4-6), and vice-versa. Considering all three factors, there is clearly the potential for a changing climate to substantially alter forest floor C storage in upland forests of the western boreal. This potential needs to be investigated with suitable process-based models.

Conclusions

This study has presented extensive new data on C storage and dynamics in the western boreal. There was strong support for the hypothesis that forest floor carbon is affected by species, stand age and climate. FFC was significantly higher for *P. tremuloides* than for *P. banksiana*. The effects of age and climate were species-specific. There was no evidence that FFC in *P. banksiana* is affected by age or climate, but in *P. tremuloides* stands, FFC was positively related to stand age and MAT, and negatively related to *P*. For both species, there was no evidence that FFC is related to biomass of understory components, other than a positive relationship with MDI in *P. banksiana* stands; further work is needed to determine why MDI is related to FFC. Evidence for relationships with mineral soil physical properties was weak: texture class or bulk density were marginally significant for *P. tremuloides*, but water holding capacity variables were not significant for either species. The statistical models give values that are generally in line with comparable data from the literature, but data on age, climate and species effects are few and sometimes contradictory. This study provides valuable new data on long-term forest floor dynamics. These findings are limited to two species in upland forests of the western boreal. Further studies are needed for other important species, such as *Picea glauca* and *Picea mariana*, to examine dynamics over successional sequences, and to define the dynamics in the moister eastern boreal.

The substantial C pool represented by the forest floor along with the effects of species, and of age and climate in the case of *P. tremuloides*, indicate that the forest floor is an important pool that may be sensitive to changing climate and needs to be explicitly modelled in C budget studies. The data and relationships presented here will be useful for constraining and validating process-based models.

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Tables

Table 4-1. Climate stations representing climatic zones 1, 2 and 3, with summary climate values based on 1951-1980 Normals (Environment Canada, 1982; Environment Canada, 1983).

Variable	Prince Albert	Fort Smith	Thompson
Zone	1	2	3
Jan temp. (°C)	-21.5	-26.8	-26.6
July temp. (°C)	17.4	16.0	15.6
Mean annual temp. (°C)	0.1	-3.3	-3.9
Growing degree days [a]	1267	992	856
Annual Rain (mm)	287	219	354
Annual Snow (cm)	122	146	233
Annual Precip. (mm)	398	349	542
Annual PET (mm) [b]	516	366	347

[a] Growing degree days were calculated by linearly interpolating temperatures between months to obtain daily values then summing temperatures in excess of 5 °C

[b] Monthly potential evapotranspiration (PET) was estimated using the method of Jensen and Haise (1963) following Bonan (1989) and summed across the year

Table 4-2. Stand age, forest floor, vegetation, mineral soil and climatic data for each one of the 80 sampled stands. Means and standard errors are shown where appropriate. FFC, forest floor carbon; Trees, Aboveground live tree C; Shrubs, Aboveground shrub C; GV, ground vegetation C; M+L, moss-plus-lichen C; MDI, moss dominance index; Txt, mineral soil texture class (a=coarse, b=medium, c=moderately fine and d=fine as described in the text); *Db*, mineral soil bulk density; AWC, mineral soil available water holding capacity; MAT, mean annual temperature from 1951-1980 Normals; *P*, annual precipitation from 1951-1980 Normals.

	Carbon pools						Mineral soil variables				Climate	
Age (yrs)	FFC (kgC m^2)	Trees (kgC m^2)	Shrubs (gC m^2)	GV (gC m^2)	M+L (gC m^2)	MDI (%)	Txt	Depth (cm)	Db (Mg m^3)	AWC (%)	MAT (°C)	P (mm)
***Pinus banksiana* Zone 1**												
16	0.8±0.1	0.8±0.2	68	3	0±0	10	a	100	1.51	1	-0.7	493
19	0.9±0.1	0.8±0.1	23	21	74±26	0	a	100	1.38	5	-0.9	516
46	1.5±0.2	3.3±0.5	11	29	69±30	81	a	100	1.39	4	-0.5	481
49	1.4±0.2	2.7±0.2	0	8	122±30	8	a	100	1.38	7	-0.6	486
55	2.1±0.3	7.0±1.2	14	15	185±50	100	a	50	1.46	7	-0.4	466
55	0.8±0.1	5.0±0.9	61	22	121±22	74	a	100	1.38	5	-0.4	469
73	1.8±0.2	6.3±1.1	92	30	104±31	100	a	100	1.36	7	-0.7	493
80	1.5±0.3	7.2±1.1	3	20	354±83	97	a	100	1.43	4	-0.4	471
80	0.7±0.1	4.5±0.5	6	10	303±40	2	a	100	1.40	4	-0.7	490
81	0.7±0.1	4.3±0.8	0	6	366±95	1	a	100	1.44	5	-0.7	489
83	1.7±0.3	7.1±1.1	32	27	128±29	100	a	100	1.37	7	-0.7	493
100	1.1±0.2	4.4±0.3	1	7	241±50	6	a	100	1.39	8	-0.6	487
105	1.1±0.1	4.1±0.4	3	39	184±59	29	a	100	1.32	8	-1.0	516
111	1.8±0.3	8.4±1.2	77	25	291±55	99	a	100	1.26	10	-1.0	518
***Pinus banksiana* Zone 2**												
16	1.0±0.2	2.7±0.2	100	3	131±64	98	a	100	1.24	8	-3.0	406
30	1.0±0.2	1.9±0.0	206	7	0±0	0	a	100	1.40	3	-3.6	401
51	1.4±0.1	1.4±0.2	11	33	0±0	9	a	100	1.25	4	-3.1	363
79	1.3±0.2	4.4±0.6	7	32	209±64	92	a	20	1.38	3	-3.6	399
85	2.4±0.3	4.2±0.1	10	0	361±74	89	a	100	1.36	8	-3.0	392
87	1.9±0.3	3.9±0.1	2	39	89±62	49	a	100	1.31	2	-3.1	366
110	1.5±0.2	6.6±0.7	19	26	309±46	100	a	100	1.28	4	-3.3	356
112	1.1±0.2	4.0±0.2	4	31	320±77	99	a	50	1.06	12	-3.9	396
125	2.1±0.5	6.3±1.0	43	18	333±91	98	a	100	1.34	14	-3.0	396
135	1.6±0.1	7.7±0.5	11	27	378±52	97	a	100	1.31	11	-3.0	397
***Pinus banksiana* Zone 3**												
30	1.3±0.1	2.1±0.5	4	11	61±32	45	a	100	1.45	2	-3.9	549
30	1.3±0.2	2.2±0.4	132	16	5±5	60	a	100	1.26	11	-3.3	520
50	1.2±0.1	3.7±0.5	110	14	168±44	35	a	100	1.22	16	-3.9	487
62	1.3±0.2	3.0±0.7	41	12	158±38	72	a	100	1.28	5	-4.7	471
63	1.0±0.1	3.1±0.3	68	22	169±50	29	a	100	1.34	6	-3.6	528
65	1.8±0.1	3.3±0.6	0	13	112±26	38	a	70	1.34	8	-4.1	507
65	1.2±0.1	3.3±0.2	88	12	73±13	91	a	100	1.40	7	-3.6	517
66	0.8±0.1	2.9±0.2	7	16	181±32	16	a	100	1.29	5	-3.8	507
67	0.8±0.1	2.6±0.8	0	13	188±51	16	a	60	1.34	11	-4.1	505
78	1.0±0.1	3.0±0.1	0	16	189±32	6	a	100	1.20	10	-3.7	511
80	1.2±0.2	3.0±0.4	5	15	309±53	4	a	100	1.39	4	-4.6	482
82	0.9±0.1	3.9±0.1	0	34	158±19	14	a	100	1.38	5	-3.1	515

Table 4-2. (continued)

	Carbon pools						Mineral soil variables				Climate	
Age (yrs)	FFC (kgC m^2)	Trees (kgC m^2)	Shrubs (gC m^2)	GV (gC m^2)	M+L (gC m^2)	MDI (%)	Txt	Depth (cm)	Db (Mg m^3)	AWC (%)	MAT (°C)	P (mm)
***Populus tremuloides* Zone 1**												
36	3.0±0.3	4.9±1.4	30	36	0±0	100	b	100	1.19	16	0.6	485
44	3.3±0.5	2.0±0.7	52	22	0±0	100	b	100	0.81	16	0.2	448
48	2.5±0.1	5.8±0.2	2	30	0±0	100	b	100	1.35	14	-0.4	462
49	3.7±0.2	4.1±0.2	24	34	37±28	100	d	100	1.39	9	-0.2	466
57	2.2±0.2	5.7±0.5	319	19	0±0	100	c	100	1.31	14	-0.6	479
58	3.6±0.4	9.4±1.9	23	26	24±24	100	c	100	1.02	14	0.7	527
58	2.6±0.3	6.4±0.6	2	19	0±0	100	b	100	1.39	11	-0.4	463
60	2.3±0.3	6.7±0.3	133	22	0±0	83	b	100	1.38	13	-0.8	499
64	2.9±0.2	5.0±0.8	148	30	0±0	75	a	100	1.41	7	-0.2	467
66	3.0±0.2	3.4±1.1	18	25	0±0	100	d	60	0.96	34	-0.6	465
67	3.9±0.4	7.1±0.2	244	33	0±0	100	b	100	1.30	11	-0.3	460
77	3.2±0.3	9.2±0.6	99	19	0±0	100	b	100	1.38	7	-0.2	462
77	2.4±0.2	10.7±2.7	117	45	0±0	100	b	100	1.27	16	-0.2	464
106	3.6±0.6	11.7±1.2	65	21	0±0	100	b	100	1.42	10	-0.2	463
106	3.7±0.4	11.7±2.0	252	53	0±0	100	c	100	1.35	13	-0.2	463
126	3.5±0.4	8.9±3.5	392	40	0±0	38	c	100	1.41	16	0.2	451
132	3.0±0.2	10.9±1.2	11	25	0±0	100	b	100	1.32	14	-0.4	486
***Populus tremuloides* Zone 2**												
14	1.7±0.2	1.0±0.1	107	20	0±0	100	b	100	1.16	21	-3.0	411
14	1.4±0.1	0.5±0.0	30	22	0±0	NA	b	25	1.32	14	-3.2	386
16	1.8±0.2	0.5±0.1	26	18	0±0	75	a	100	1.33	15	-3.0	415
49	1.8±0.2	2.5±0.1	79	22	0±0	80	b	25	1.13	14	-3.3	405
49	2.9±0.2	4.0±0.8	94	38	0±0	100	b	100	1.08	21	-3.3	397
50	1.6±0.1	4.5±1.1	36	19	0±0	100	b	25	1.40	12	-3.3	396
52	3.4±0.2	2.0±0.2	46	16	0±0	NA	d	20	1.03	13	-3.1	359
54	3.4±0.3	4.3±0.6	126	25	0±0	NA	a	100	0.74	13	-3.1	370
58	2.8±0.2	3.2±0.1	101	36	0±0	NA	a	100	0.92	8	-3.1	352
58	2.1±0.2	3.6±0.9	148	31	0±0	100	b	86	1.21	8	-3.2	366
58	1.7±0.3	4.2±1.1	50	29	0±0	NA	b	100	1.12	5	-3.2	359
66	4.0±0.4	7.2±1.0	26	33	14±14	100	a	100	1.36	8	-3.0	385
103	4.6±0.4	5.4±2.4	229	8	0±0	31	c	100	0.78	13	-2.4	396
105	4.0±0.3	7.1±2.0	94	21	0±0	100	b	100	1.25	7	-3.1	365
120	3.6±0.4	7.8±0.0	163	35	30±30	NA	b	100	0.78	9	-2.4	396
149	4.3±0.4	8.3±1.2	33	32	0±0	100	b	77	0.97	17	-3.0	411
***Populus tremuloides* Zone 3**												
28	1.5±0.2	1.4±0.2	959	18	0±0	27	d	100	1.01	13	-4.0	519
50	2.2±0.1	3.5±0.4	93	19	29±19	100	d	100	0.98	19	-3.3	504
50	1.7±0.2	2.8±0.6	16	23	12±12	100	d	100	0.91	21	-3.1	500
53	2.0±0.1	4.3±0.4	28	18	0±0	63	d	100	0.99	19	-3.1	500
63	2.1±0.1	4.3±0.9	374	28	0±0	38	d	100	1.06	18	-4.0	516
65	2.5±0.2	5.1±0.4	224	15	0±0	85	d	100	0.94	13	-3.5	515
73	2.8±0.3	5.6±0.5	81	0	5±5	100	d	100	0.85	12	-2.3	468
88	2.4±0.2	7.1±1.5	325	0	24±15	100	d	100	1.06	11	-3.3	508
103	3.1±0.4	7.4±1.5	228	0	0±0	100	c	100	1.02	18	-3.0	497
107	1.9±0.2	5.1±0.5	573	0	0±0	100	d	100	0.97	18	-3.3	513
112	2.5±0.4	8.2±0.8	405	0	2±2	100	d	100	0.88	18	-3.0	496

Table 4-3. ANCOVA table and coefficients showing relationship between percent carbon of forest floor samples (%C) and percent organic matter (%OM), amount of organic matter (OM) (kg m^{-2}) and climatic zone (ZONE) (r^2= 0.94). *df*, degrees of freedom; *F*, F-statistic for null hypothesis; Sig., observed significance level of F-statistic.

Source	Sum of Squares	df	*F*	Sig.	Coefficients
Model	6261	4	210	.000	
Intercept	59	1	8	.007	2.652
OM	53	1	7	.010	-0.100
%OM	4682	1	628	.000	0.541
%OM*ZONE	138	2	9	.000	Zone1=-0.0199 Zone2=0 Zone3=-0.0656
Error	410	55			

Table 4-4. Carbon storage (kgC m^{-2}) in aboveground live vegetation and the forest floor averaged across zones and ages for the stands sampled in this study.

Component	*P. banksiana*	*P. tremuloides*
Total C	5.58	8.54
..Trees	4.03	5.54
..Shrubs	0.035	0.150
..Total ground vegetation	0.019	0.026
....Dwarf shrubs & forbs	0.016	0.015
....Grasses	0.003	0.010
....Legumes	0.000	0.001
..Moss-plus-lichen	0.179	0.004
..Forest floor	1.31	2.82

Table 4-5. Characteristics of the six chronosequences (means are shown with standard deviations. NA, not applicable).

	P. banksiana			*P tremuloides*		
	Zone 1	Zone 2	Zone 3	Zone 1	Zone 2	Zone 3
No. of stands	14	10	12	17	17	11
Min. and max. age (years)	16-111	16-135	30-82	36-132	14-149	28-112
Species dominance (%)	99±3	100±1	93±6	93±8	93±10	98±3
Mean annual temperature (°C)	-0.7±0.2	-3.2±0.3	-3.9±0.5	-0.2±0.4	-3.0±0.3	-3.3±0.5
Annual precipitation (mm)	491±17	387±18	508±21	471±19	385±20	503±14
Mineral soil						
Bulk density (Mg m^{-3})	1.39±0.06	1.29±0.10	1.33±0.08	1.27±0.18	1.09±0.21	0.97±0.07
Available water holding capacity (g g^{-1})	6%±2%	7%±4%	7%±4%	14%±6%	13%±5%	16%±3%
No. of stands in each texture class[a]	14-0-0-0	10-0-0-0	12-0-0-0	1-10-4-2	5-10-1-1	0-0-1-10
Shrubs (gC m^{-2})	28±32	41±65	38±49	114±120	89±57	301±280
Dwarf shrubs & forbs (gC m^{-2})	15±9	16±12	16±5	16±4	11±8	18±6
Grasses (gC m^{-2})	4±4	4±4	0±1	10±8	14±5	3±5
Legumes (gC m^{-2})	0.0±0.2	0.4±0.8	0.0±0.0	1.5±1.7	1.9±1.5	0.2±0.5
Moss dominance (%)	50±45	73±39	35±27	NA	NA	NA
Forest floor (kgC m^{-2})	1.29±0.47	1.52±0.49	1.17±0.27	3.09±0.53	2.93±1.16	2.26±0.47
Linear regression of tree C against stand age						
Coefficient (gC m^{-2} yr^{-1})	67.2	50.6	47.1	97.8	64.5	69.0
r-square	0.47	0.74	0.47	0.53	0.80	0.81
Linear regression of moss/lichen layer C against stand age						
Coefficient (gC m^{-2} yr^{-1})	2.7	2.6	2.5	NA	NA	NA
r-square	0.49	0.63	0.51			

[a] texture classes are coarse, medium, moderately fine, and fine as described in the text.

Table 4-6. ANCOVA table and coefficients for the effect of species, climatic zone and natural logarithm of stand age (lnAGE) on natural logarithm of FFC ($r^2 = 0.73$). *df*, degrees of freedom; *F*, F-statistic for null hypothesis; Sig., observed significance level of F-statistic.

Source	Sum of Squares	df	*F*	Sig.	Coefficients
Model	14.08	4	51.9	0.000	
Intercept	0.34	1	5.0	0.028	-0.510732
lnAGE	1.62	1	23.9	0.000	0.32349
Species*lnAGE	11.14	1	164.5	0.000	*P.tremuloides*=0 *P.banksiana*=-0.180850
Zone*lnAGE	0.78	2	5.7	0.005	Zone1=0.046197 Zone2=0.057820 Zone3=0
Error	5.08	75			

Table 4-7. Pearson's correlation coefficients (upper right) and the corresponding significance levels (lower left) for a selection of stand variables. FFC, forest floor carbon; DS&F, dwarf shrubs and forbs; M+L, moss-plus-lichen; MDI, moss dominance index; *Db*, mineral soil bulk density; AWC, available water holding capacity; MAT, mean annual temperature 1951-1980; *P*, annual precipitation 1951-1980.

	Age	Tree	Shrub	M+L	MDI	DS&F	Grass	Legumes	FFC	*Db*	AWC	MAT	*P*
Age		0.70	0.04	0.34	0.18	0.15	0.04	0.01	0.31	-0.10	0.05	0.06	-0.08
Tree	0.000		0.10	-0.02	0.51	0.11	0.19	0.13	0.56	0.02	0.13	0.46	0.05
Shrub	0.706	0.382		-0.36	0.03	-0.05	-0.02	-0.08	0.19	-0.33	0.27	-0.12	0.17
M+L	0.002	0.885	0.001		-0.25	0.16	-0.34	-0.31	-0.52	0.37	-0.41	-0.10	0.05
MDI	0.123	0.000	0.794	0.035		0.43	0.29	0.29	0.54	-0.26	0.42	0.20	-0.26
DS&F	0.175	0.311	0.629	0.162	0.000		-0.10	0.01	-0.04	0.03	0.17	0.02	0.24
Grass	0.730	0.095	0.827	0.002	0.013	0.390		0.55	0.54	-0.21	0.17	0.24	-0.47
Legume	0.958	0.233	0.499	0.004	0.012	0.902	0.000		0.44	-0.12	0.22	0.13	-0.35
FFC	0.004	0.000	0.100	0.000	0.000	0.756	0.000	0.000		-0.42	0.43	0.30	-0.28
Db	0.394	0.867	0.003	0.001	0.024	0.818	0.064	0.279	0.000		-0.59	0.27	0.16
AWC	0.673	0.240	0.014	0.000	0.000	0.131	0.127	0.046	0.000	0.000		0.03	0.05
MAT	0.588	0.000	0.299	0.368	0.082	0.831	0.035	0.239	0.006	0.016	0.810		0.21
P	0.506	0.684	0.136	0.687	0.024	0.034	0.000	0.001	0.013	0.169	0.636	0.066	

Table 4-8. Regression models for natural logarithm of FFC for *P. tremuloides* and *P. banksiana* using significant independent variables that explain the most variation. lnAGE, natural logarithm of stand age (years); MAT, Mean Annual Temperature (°C); *P*, annual precipitation (mm); *Db*, mineral soil bulk density (Mg m^{-3}); asMDI, arcsin(sqrt(Moss Density Index)); *B*, regression coefficient; SE *B*, standard error of *B*; *T*, test of null hypothesis; Sig *T*, the 2-tailed observed significance level of *T*.

Variable	*B*	SE *B*	*T*	Sig *T*
P. tremuloides **regression model (F=18; n=44; r^2=0.64)**				
Constant	1.329	0.463	2.871	0.007
lnAge	0.310	0.058	5.305	0.000
MAT	0.120	0.024	4.958	0.000
P	-0.00212	0.001	-3.541	0.001
Db	-0.384	0.165	-2.330	0.025
P. banksiana **regression model (F=23; n=36; r^2=0.41)**				
Constant	-0.0905	0.077	-1.173	0.249
AsMDI	0.378	0.079	4.813	0.000

Figures

Figure 4-1. Study area showing climatic zones in which sampled stands were located.

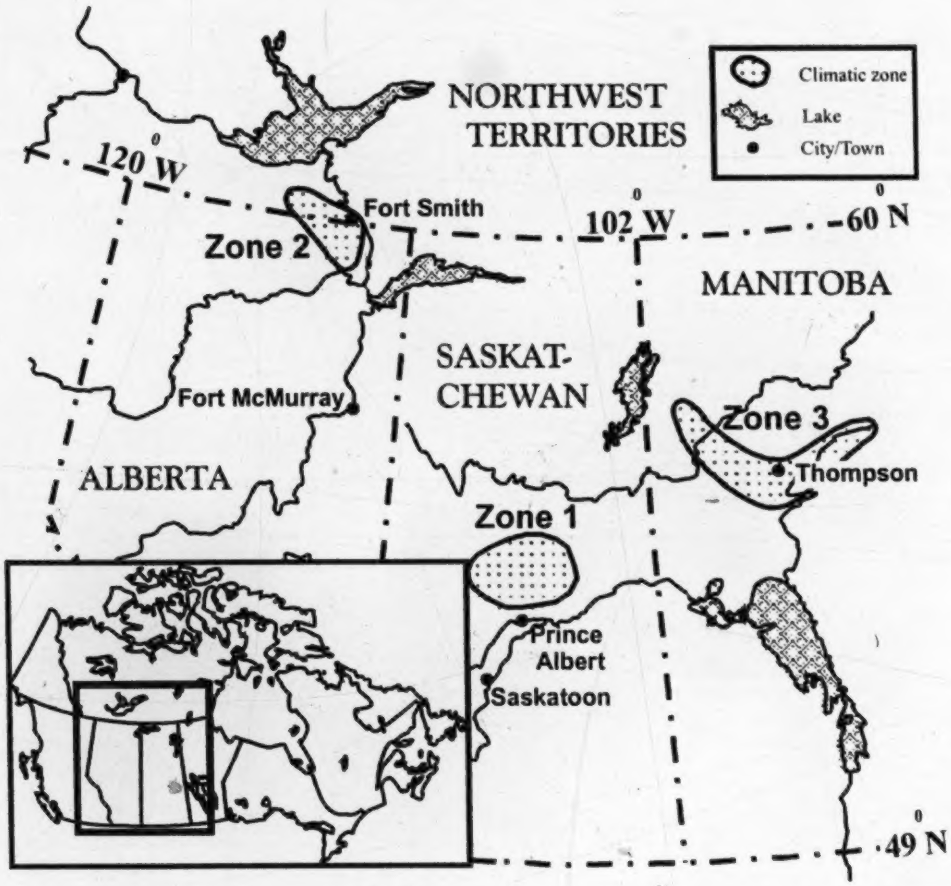

Climatic zone
Lake
City/Town
NORTHWEST TERRITORIES
120° W
102° W
60° N
49° N
Fort Smith
Zone 2
MANITOBA
SASKAT-CHEWAN
Fort McMurray
Zone 3
Thompson
ALBERTA
Zone 1
Prince Albert
Saskatoon

Figure 4-2. Relationship between total carbon content of forest floor and organic matter content as determined by loss-on-ignition for each climatic zone. For comparison, the dotted line represents the commonly-used 58% assumption, and the solid line plots the relationship determined by David (1988).

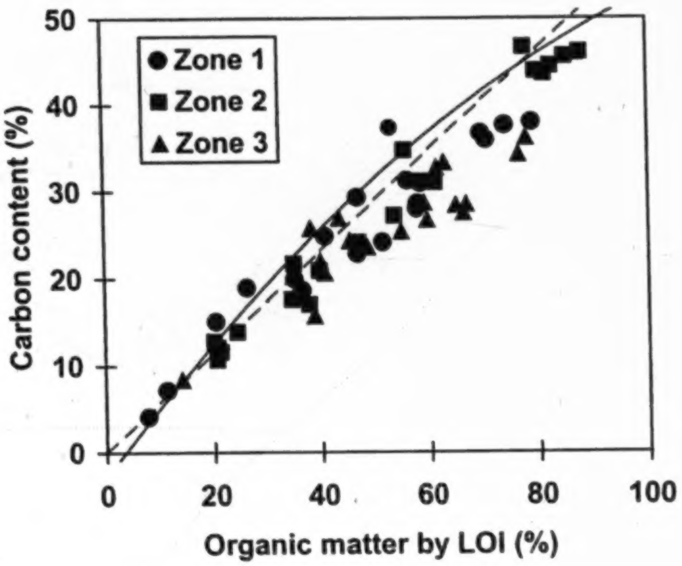


Figure 4-3. Relationship between aboveground live tree carbon and stand age for each species and climatic zone. Triangles and dashed lines represent *P. tremuloides*; circles and solid lines represent *P. banksiana*; error bars represent standard errors of the mean. R^2 and slopes of fitted regression lines are given in Table 4-5.

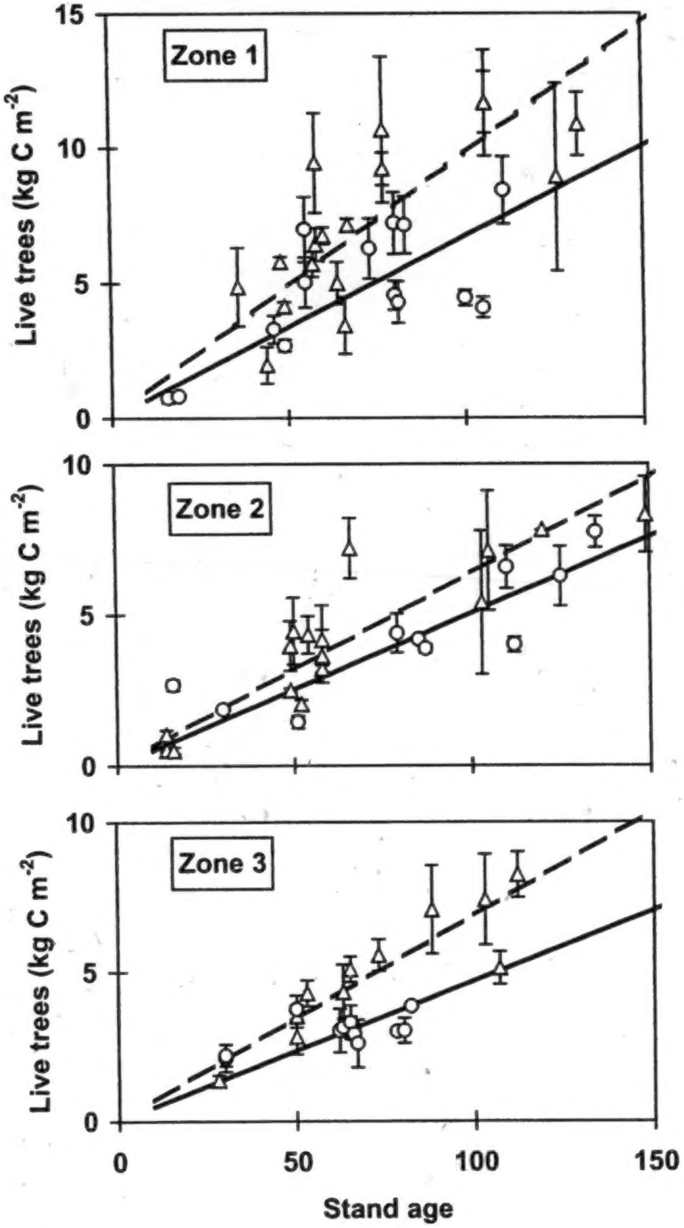


Figure 4-4. *P. banksiana* moss-plus-lichen carbon versus stand age for each climatic zone.

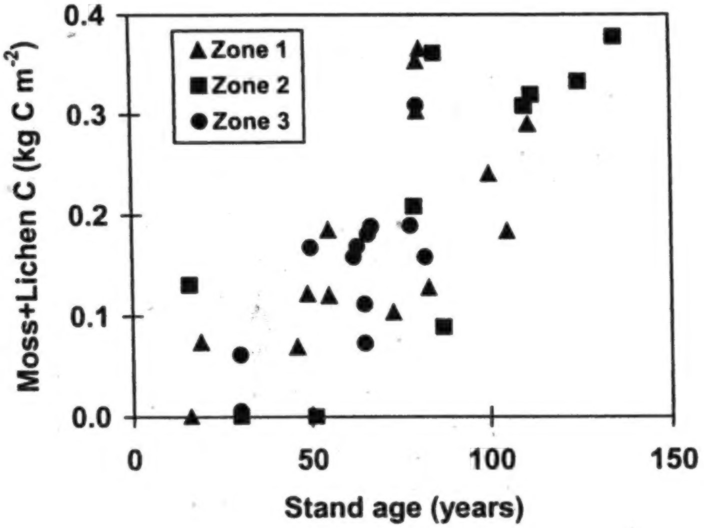


Figure 4-5. Dynamics of the decomposing coarse woody debris (rotten log) component of the forest floor by age class and species.

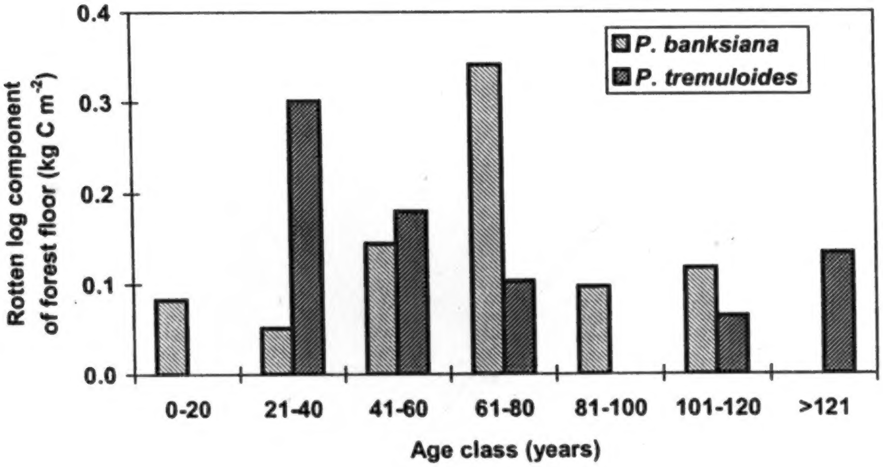


Figure 4-6. Relationships between FFC and stand age (AGE) for each climatic zone and species. Both FFC and AGE have been natural log transformed. Predictions from ANCOVA model of Table 6 are shown by lines. Triangles and dashed lines represent *P. tremuloides*; circles and solid lines represent *P. banksiana*; error bars represent standard errors of the mean.

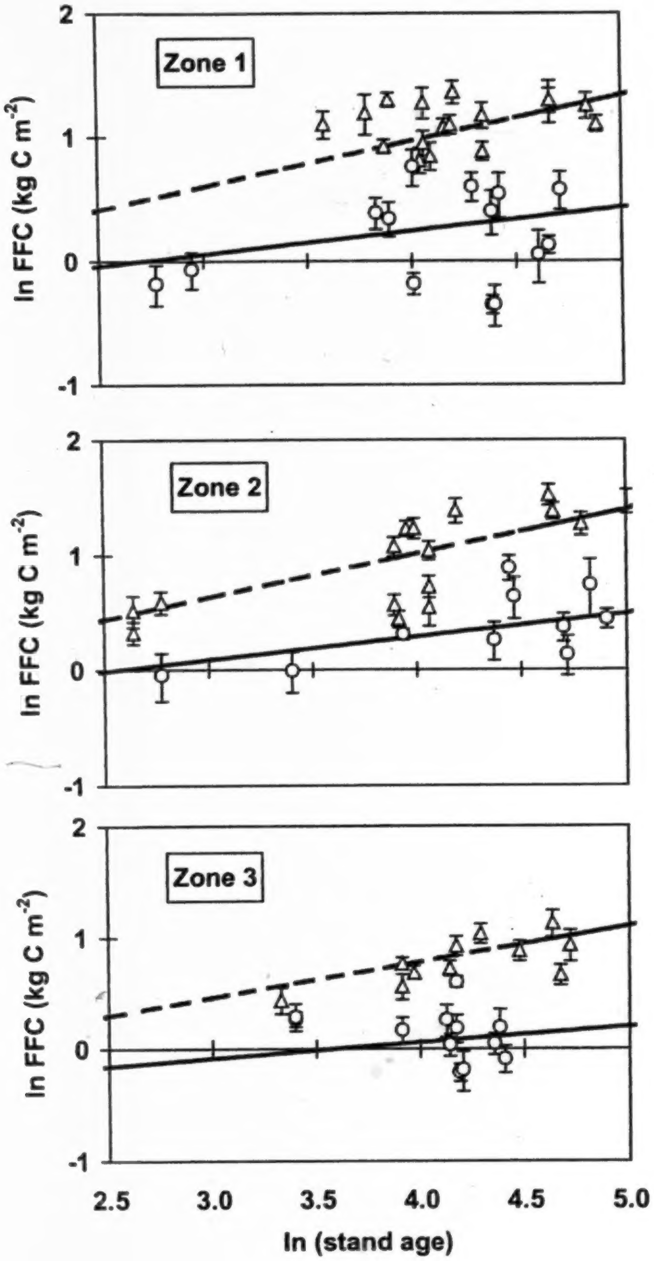


Figure 4-7. Effect of AGE, MAT and *P* on FFC for *P. tremuloides*. Data points are the mean of observed FFC plus residuals from regressions of (a) ln(FFC) against MAT, *P* and *Db*, (b) ln(FFC) against ln(AGE), *P* and *Db* and (c) ln(FFC) against ln(AGE), MAT and *Db*. Linear regression line fits for these data points, along with the models and r^2, are shown on the plots.

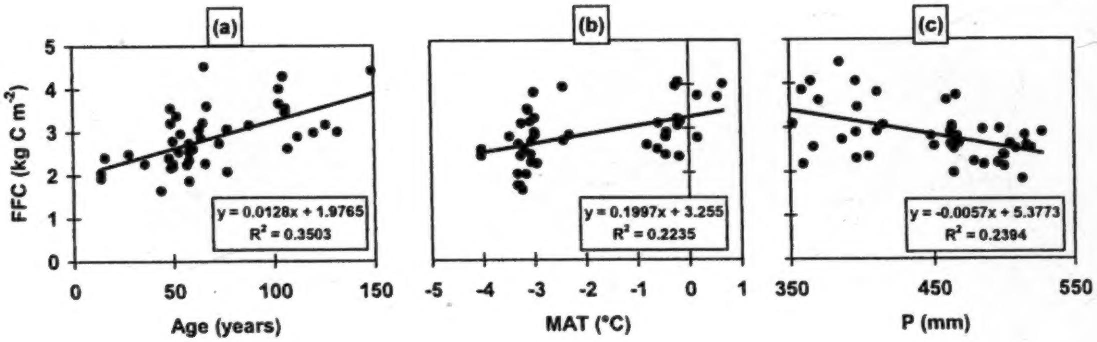


Figure 4-8. Effect of moss dominance index (MDI) on *P. banksiana* FFC. Stand means and standard errors are shown by circles and error bars. Line is the fitted regression model from Table 8. lnFFC, natural logarithm of FFC; asMDI, arcsine square root of MDI.

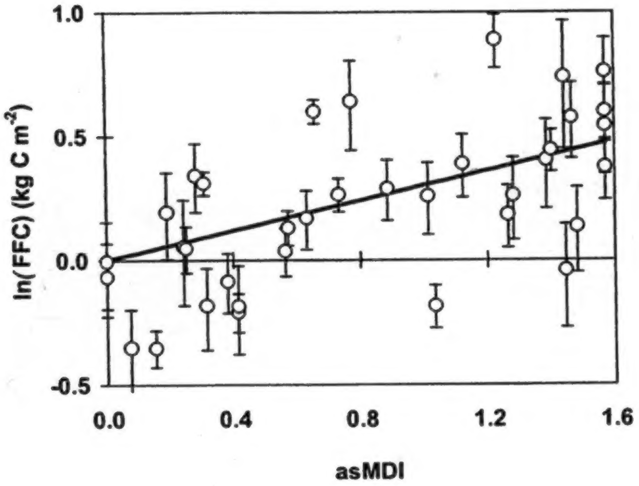
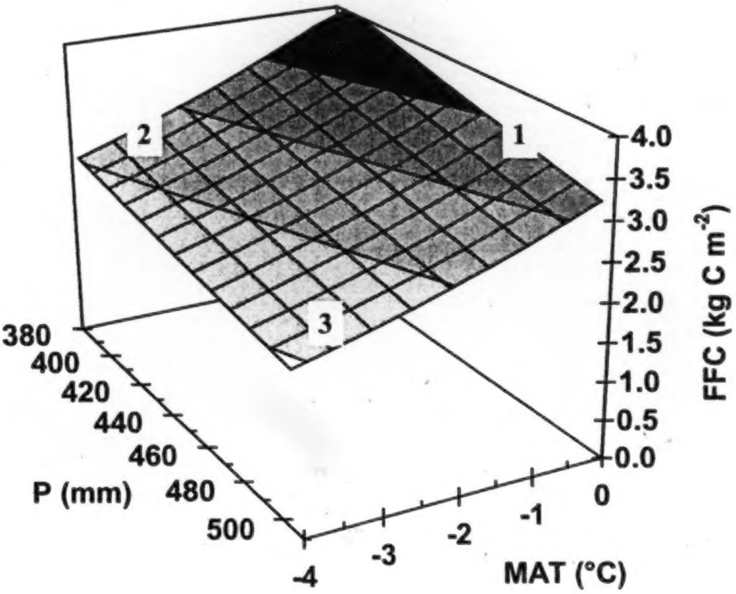


Figure 4-9. Plot of the regression model for *P. tremuloides* FFC showing the interactive effects of MAT and *P* for a stand age of 75 years and mineral soil bulk density of 1.13. The numbered squares indicate the average MAT and *P* values for the *P. tremuloides* stands within the climatic zone given by the number.



References

Agriculture Canada Expert Committee on Soil Survey, 1987. The Canadian System of Soil Classification. Publ. 1646. Agric. Can., Ottawa, Ontario, Canada.

Alban, D.H., 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. Soil Sci. Soc. Am. J., 46: 853-861.

Alberta Forest Service, 1985. Alberta Phase 3 Forest Inventory: Yield Tables for Unmanaged Stands. Dept. Report 60a. Alberta Energy and Natural Resources, Edmonton, Canada.

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G. and Vinson, T.S., 1993. Boreal forests and tundra. Water, Air, Soil Pollut., 70: 39-53.

Berg, B. and Ekbohm, G., 1991. Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. Can. J. Bot., 69: 1449-1456.

Berg, B., McClaugherty, C., Virzo De Santo, A., Johansson, M.-B. and Ekbohm, G., 1995. Decomposition of litter and soil organic matter: can we distinguish a mechanism for soil organic matter buildup? Scand. J. For. Res., 10: 108-119.

Bergeron, Y. and Flannigan, M.D., 1995. Predicting the effects of climate change on fire frequency in the southeastern Canadian boreal forest. Water, Air, Soil Pollut., 82: 437-444.

Black, T.A., denHartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nesic, Z., Lee, X., Chen, S.G., Staebler, R. and Novak, M.D., 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. Global Change Biol., 2: 219-229.

Bonan, G.B., 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecol. Model., 45: 275-306.

Bonan, G.B. and Korzuhin, M.D., 1989. Simulation of moss and tree dynamics in the boreal forests of interior Alaska. Vegetatio, 84: 31-44.

Bonan, G.B. and Shugart, H.H., 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Syst., 20: 1-28.

Botkin, D.B. and Simpson, L.G., 1990. Biomass of the north American boreal forest, a step toward accurate global measures. Biogeochem., 9: 161-174.

Bradshaw, R.H.W. and Zackrisson, O., 1990. A two thousand year history of a northern Swedish boreal forest stand. J. Veg. Sci., 1: 519-528.

Brady, N.C., 1990. The Nature and Properties of Soils. 10th edition. Macmillan Publishing Company, New York, N.Y. 621 pp.

Burton, P.J. and Cumming, S.G., 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water, Air, Soil Pollut., 82: 401-414.

Chapman, W.L. and Walsh, J.E., 1993. Recent variations of sea ice and air temperature at high latitudes. Bull. Am. Meteorol. Soc., 74: 33-47.

Ciais, P., Tans, P.P., Trolier, M., White, J.W.C. and Francey, R.J., 1995. A large northern hemisphere terrestrial CO_2 sink indicated by the $^{13}C/^{12}C$ ratio of atmospheric CO_2. Science, 269: 1098-1102.

Clark, J.S., 1988. Effect of climate change on fire regimes in northwestern Minnesota. Nature, 334: 233-234.

Clark, J.S., 1990. Fire and climate change during the last 750 yr in northwestern Minnesota. Ecol. Monogr., 60(2): 135-159.

David, M.B., 1988. Use of loss-on-ignition to assess soil organic carbon in forest soils. Commun. Soil Sci. Plant Anal., 19(14): 1593-1599.

Ecoregions Working Group of Canada, 1989. Ecoclimatic Regions of Canada. Ecol. Land Classif. Ser. 23. Environ. Can. Wildl. Serv., Can. Comm. Ecol. Land Classif., Ottawa, Ontario, Canada.

Environment Canada, 1982. Canadian Climate Normals 1951-1980. Temperature and Precipitation, The North - Y.T. and N.W.T. Atmospheric Environment Service, Environment Canada, Downsview, Ontario, Canada. 56 pp.

Environment Canada, 1983. Canadian Climate Normals 1951-1980. Temperature and Precipitation, Prairie Provinces. Atmospheric Environment Service, Environment Canada, Downsview, Ontario, Canada. 429 pp.

Evert, F., 1985. Systems of equations for estimating ovendry mass of 18 Canadian tree species. Inf. Rep. PI-X-59. PNFI, Can. For. Serv., Chalk River, Ontario, Canada.

Forestry Canada Fire Danger Group, 1992. Development and structure of the Canadian Forest Fire Behaviour Prediction System. Inf. Rep. ST-X-3. Forestry Canada, Ottawa, Canada.

Foster, N.W., Morrison, I.K., Hazlett, P.W. and Hogan, G.D., 1995. Carbon and nitrogen cycling within mid- and late-rotation jack pine. In: McFee, W.W. and Kelly, J.M., (Editors). Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Inc., Madison, Wisconsin, USA, pp. 355-375.

Francey, R.J., Tans, P.P., Allison, C.E., Enting, I.G., White, J.W.C. and Trolier, M., 1995. Changes in oceanic and terrestrial carbon uptake since 1982. Nature, 373: 326-330.

Gorshkov, V.V., Bakkal, I.J. and Stavrova, N.I., 1996. Postfire recovery of forest litter in Scots Pine forests in two different regions of Boreal Zone. Silva Fennica, 30(2-3): 209-219.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J. and Stow, T.K., 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophy. Res., 102(D24): 29029-29041.

Gray, S.L., 1995. A descriptive forest inventory of Canada's forest regions. Inf. Rep. PI-X-122. Can. For. Serv., Chalk River, Ontario, Canada.

Grigal, D.F., Brovold, S.L., Nord, W.S. and Ohmann, L.F., 1989. Bulk density of surface soils and peat in the North Central United States. Can. J. Soil Sci., 69: 895-900.

Grigal, D.F. and Ohmann, L.F., 1992. Carbon storage in upland forests of the Lake States. Soil Sci. Soc. Am. J., 56: 935-943.

Halliwell, D.H. and Apps, M.J., 1997a. BOReal Ecosystem-Atmosphere Study (BOREAS) biometry and auxiliary sites: overstory and understory data. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, Canada. 254 pp.

Halliwell, D.H. and Apps, M.J., 1997b. BOReal Ecosystem-Atmosphere Study (BOREAS) biometry and auxiliary sites: soils and detritus data. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, Canada. 235 pp.

Harden, J.W., Sundquist, E.T., Stallard, R.F. and Mark, R.K., 1992. Dynamics of soil carbon during the deglaciation of the Laurentide Ice Sheet. Science, 258: 1921-1924.

Hausenbuiller, R.L., 1985. Soil Science Principles and Practices. 3rd edition. Wm. C. Brown Publishers, Dubuque, Iowa. 610 pp.

Heathcott, M.J. and Cornelsen, S.C., 1994. Options for fire management in Wood Buffalo National Park. In: Duncan, T.A., Forster, W.A.D. and Lanoville., R.A., (Editors). Managing Fire Dependent Ecosystems: Options and Technologies. Proceedings from 1992 Interior West Fire Council Annual Meeting October 27-29, 1992, Yellowknife, NWT. Govt. Northwest Territories, pp. 75-85.

Heinselman, M.L., 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res., 3: 329-382.

Hogg, T.H., 1994. Climate and the southern limit of the western Canadian boreal forest. Can. J. For. Res., 24: 1835-1845.

Huang, W.Z. and Schoenau, J.J., 1996. Forms, amounts and distribution of carbon, nitrogen, phosphorus and sulfur in a boreal aspen forest soil. Can. J. Soil Sci., 76: 373-385.

Isaev, A., Korovin, G., Samolodchikov, D., Utkin, A. and Pryaznikov, A., 1995. Carbon stock and deposition in phytomass of the Russian forests. Water, Air, Soil Pollut., 82: 247-256.

Jensen, M.E. and Haise, H.R., 1963. Estimating evapotranspiration from solar radiation. J. Irrig. Drain. Div. Am. Soc. Civ. Eng., 89: 15-41.

Johnson, E.A., 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. Ecology, 62: 200-215.

Johnson, E.A. and Gutsell, S.L., 1994. Fire frequency models, methods and interpretations. Adv. Ecol. Res., 25: 239-287.

Jones, P.D., 1994. Hemispheric surface temperature variations: a reanalysis and an upgrade to 1993. J. Clim., 7: 1794-1802.

Karjalainen, T., 1996. The carbon sequestration potential of unmanaged forest stands in Finland under changing climatic conditions. Biomass Bioenergy, 10(5-6): 313-329.

Kasischke, E.S., Christensen Jr., N.L. and Stocks, B.J., 1995. Fire, global warming, and the carbon balance of boreal forests. Ecol. Appl., 5: 437-451.

Kauppi, P.E., Posch, M., Hanninen, P., Henttonen, H.M., Ihalainen, A., Lappalainen, E., Starr, M. and Tamminen, P., 1997. Carbon reservoirs in peatlands and forests in the boreal regions of Finland. Silva Fennica, 31(1): 13-25.

Kauppi, P.E., Tomppo, E. and Ferm, A., 1995. C and N storage in living trees within Finland since 1950's. Plant Soil, 168-169: 633-638.

Keeling, C.D., Chin, J.F.S. and Whorf, T.P., 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. Nature, 382: 146-149.

Kimmins, J.P., 1987. Forest Ecology. Macmillan Publishing Company, New York. 531 pp.

Kolchugina, T.P. and Vinson, T.S., 1993a. Comparison of two methods to assess the carbon budget of forest biomes in the former Soviet Union. Water, Air, Soil Pollut., 70: 207-221.

Kolchugina, T.P. and Vinson, T.S., 1993b. Equilibrium analysis of carbon pools and fluxes of forest biomes in the former Soviet Union. Can. J. For. Res., 23: 81-88.

Krause, K., 1998. Forest floor mass and nutrients in two chronosequences of plantations: Jack pine vs. black spruce. Can J. Soil Sci., 78(1): 77-83.

Kurz, W.A., Apps, M.J., Beukema, S.J. and Lekstrum, T., 1995. Twentieth century carbon budget of Canadian forests. Tellus, 47B: 170-177.

Kurz, W.A., Apps, M.J., Webb, T.M. and McNammee, P.J., 1992. The carbon budget of the Canadian Forest Sector: Phase I. Inf. Rep. NOR-X-326. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta, Canada.

Landhäusser, S.M. and Wein, R.W., 1993. Postfire vegetation recovery and tree establishment at the Arctic treeline: climate-change vegetation response hypotheses. J. Ecol., 81: 665-672.

Larsen, C.P.S., 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeogr., 24: 663-673.

Larsen, C.P.S. and MacDonald, G.M., 1995. Relations between tree-ring widths, climate, and annual area burned in the boreal forest of Alberta. Can. J. For. Res., 25: 1746-1755.

Lenihan, J.M. and Neilson, R.P., 1995. Canadian vegetation sensitivity to projected climatic change at three organizational levels. Clim. Change, 30: 27-56.

Liski, J., Ilvesniemi, H., Mäkelä, A. and Starr, M., 1998. Model analysis of the effects of soil age, fires and harvesting on the carbon storage of boreal forest soils. Eur. J. Soil Sci., 49(3): 407-416.

Liski, J. and Westman, C.J., 1995. Density of organic carbon in soil at coniferous forest sites in southern Finland. Biogeochem., 29: 183-197.

Liski, J. and Westman, C.J., 1997a. Carbon storage in forest soil of Finland: 1. Effect of thermocline. Biogeochem., 36: 239-260.

Liski, J. and Westman, C.J., 1997b. Carbon storage in forest soil of Finland; 2. Size and regional patterns. Biogeochem., 36: 261-274.

MacLean, D.A. and Wein, R.W., 1977. Nutrient accumulation for postfire jack pine and hardwood succession patterns in New Brunswick. Can. J. For. Res., 7: 562-578.

Morrison, I.K., Foster, N.W. and Hazlett, P.W., 1993. Carbon reserves, carbon cycling, and harvesting effects in three mature forest types in Canada. N. Z. J. For. Sci., 23: 403-412.

Murphy, P.J., 1985. Methods for evaluating the effects of forest fire management in Alberta. Ph.D. thesis, Faculty of Forestry, University of British Columbia, Vancouver, B.C. 167 pp.

Nalder, I.A. and Wein, R.W., 1998a. A new forest floor corer for rapid sampling, minimal disturbance and adequate precision. Silva Fennica, 32(4): 373-382.

Nalder, I.A. and Wein, R.W., 1998b. Spatial interpolation of climatic Normals: test of a new method in the Canadian boreal forest. Agric. For. Meteorol., 92(4): 211-225.

Nalder, I.A. and Wein, R.W., 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochem. Cycles, 13(4): 951-968.

Ohmann, L.F., Grigal, D.F. and Rogers, L.L., 1981. Estimating plant biomass for undergrowth species of northeastern Minnesota forest communities. Gen. Tech. Rep. NC-61. USDA For. Serv., N. Centr. For. Exp. Stn., St. Paul, Minnesota.

Paré, D. and Bergeron, Y., 1996. Effect of colonization tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Can. J. For. Res., 26(6): 1022-1031.

Paré, D., Bergeron, Y. and Camiré, C., 1993. Changes in the forest floor of Canadian boreal forest after disturbance. J. Veg. Sci., 4: 811-818.

Pastor, J. and Post, W.M., 1988. Response of northern forests to CO_2-induced climatic change. Nature, 334: 55-58.

Pickett, W.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E., (Editor). Long Term Studies in Ecology: Approaches and Alternatives. Springer-Verlag, New York, pp. 110-135.

Post, W.M., Emanuel, W.R., Zinke, P.J. and Stangenberger, A.G., 1982. Soil carbon pools and world life zones. Nature, 289: 156-159.

Price, D.T., Curry, S.R., Halliwell, D.H., Apps, M.J. and Kurz, W.A., 1997. Comprehensive assessment of carbon stocks and fluxes in a boreal-cordilleran forest management unit. Can. J. For. Res., 27: 2005-2016.

Protz, R., Ross, G.J., Martini, I.P. and Terasmae, J., 1984. Rate of podzolic soil formation near Hudson Bay, Ontario. Can. J. Soil Sci., 64: 31-49.

Protz, R., Ross, G.J., Martini, I.P. and Terasmae, J., 1988. Podzolic soil development in the Southern James Bay lowlands, Ontario. Can. J. Soil Sci., 68: 287-305.

Randerson, J.T., Thompson, M.V., Conway, T.J., Fung, I.Y. and Field, C.B., 1997. The contribution of terrestrial sources and sinks to trends in the seasonal cycle of atmospheric carbon dioxide. Global Biogeochem. Cycles, 11(4): 535-560.

Rowe, J.S., 1972. Forest Regions of Canada. Can. For. Serv., Dep. Environ., Ottawa, Ontario, Canada. 172 pp.

Schimel, D., Alves, D., Enting, I., Heimann, M., Joos, F., Raynaud, D., Wigley, T., Prather, M., Derwent, R., Ehhalt, D., Fraser, P., Sanhueza, E., Shou, X., Jonas, P., Charlson, R., Rodhe, H., Sadasivan, S., Shine, K.P., Fouquart, Y., Ramaswamy, V., Solomon, S., Srinivasan, J., Albritton, D., Derwent, R., Isaksen, I., Lal, M. and Wuebbles, D., 1996. Radiative forcing of climate change. In: Houghton, J.T., Meira Filho, J.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K., (Editors). Climate Change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, UK, pp. 65-131.

Siltanen, R.M., Apps, M.J., Zoltai, S.C., Mair, R.M. and Strong, W.L., 1997. A soil profile and organic carbon data base for Canadian forest and tundra mineral soils. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, Canada. 50 pp.

Simmons, J.A., Fernandez, I.J., Briggs, R.D. and Delaney, M.T., 1996. Forest floor carbon pools and fluxes along a regional climate gradient in Maine, USA. For. Ecol. Man., 84: 81-95.

Smith, W.B. and Brand, G.J., 1983. Allometric biomass equations for 98 species of herbs, shrubs, and small trees. Res. Note NC-299. USDA For. Serv., N. Centr. For. Exp. Stn., St. Paul, Minnesota.

SPSS Inc., 1993. SPSS for Windows: Base System User's Guide, Release 6.0. SPSS Inc., Chicago, Illinois. 828 pp.

SPSS Inc., 1996. SPSS Advanced Statistics 7.0 Update. SPSS Inc., Chicago, Illinois. 166 pp.

Stoeckeler, J.H., 1961. Organic layers in Minnesota aspen stands and their role in soil improvement. For. Sci., 7: 66-71.

Tamm, C.O., 1964. Growth of *Hylocomuim splendens* in relation to tree canopy. Bryologist, 67: 423-426.

Tarnocai, C., 1998. The amount of organic carbon in various soil orders and ecological provinces in Canada. In: Lal et al., R., (Editor). Soil Processes and the Carbon Cycle: Advances in Soil Science. CRC Press, Boca Raton, Florida, pp. 81-92.

Thompson, I.D., Flannigan, M.D., Wotton, B.M. and Suffling, R., 1998. The effects of climate change on landscape diversity: An example in Ontario forests. Environ. Monit. Assess., 49(2-3): 213-233.

Trumbore, S.E. and Harden, J.W., 1997. Input, accumulation, and turnover of carbon in soils of the BOREAS Northern Study Area. J. Geophy. Res., 102(D24): 28817-28830.

van Cleve, K. and Noonan, L.L., 1975. Litterfall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. Can. J. For. Res., 5: 626-639.

van Cleve, K., Olivier, L., Schlentner, R., Viereck, L.A. and Dyrness, C.T., 1983. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res., 13: 747-766.

Van Wagner, C.E., 1978. Age-class distribution and the forest fire cycle. Can. J. For. Res., 8: 220-227.

Van Wagner, C.E., 1983. Fire behaviour in northern conifer forests and shrublands. In: Wein, R.W. and McLean, D.A., (Editors). The Role of Fire in Northern Circumpolar Ecosystems. John Wiley & Sons, Chichester, UK, pp. 65-80.

Viereck, L.A., 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. In: Wein, R.W. and McLean, D.A., (Editors). The Role of Fire in Northern Circumpolar Ecosystems. John Wiley & Sons, Chichester, UK, pp. 201-220.

Wardle, D.A., Zackrisson, O., Hörnberg, G. and Gallet, C., 1997. The influence of island area on ecosystem properties. Science, 277: 1296-1299.

Weber, M.G. and Flannigan, M.D., 1997. Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. Environ. Rev., 5: 145-166.

Wein, R.W., 1990. The importance of wildfire to climate change - hypotheses for the taiga. In: Goldammer, J.G. and Jenkins, M.V., (Editors). Fire in Ecosystem Dynamics: Mediterranean and northern perspectives. SPB Academic Publishing, The Hague, The Netherlands, pp. 185-190.

Zackrisson, O., Nilsson, M.-C. and Wardle, D.A., 1996. Key ecological function of charcoal from wildfire in the boreal forest. Oikos, 77: 10-19.

Zar, J.H., 1984. Biostatistical Analysis. 2nd edition. Prentice-Hall Inc., Englewood Cliffs NJ. 718 pp.

Zinke, P.J., Stangenberger, A.G., Post, W.M., Emanuel, W.R. and Olson, J.S., 1986. Worldwide organic soil carbon and nitrogen data. Report NDP-018. Carbon Dioxide Inf. Cent., Oak Ridge Natl. Lab., Oak Ridge, Tennessee.

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5. Can patch models replicate observed stand dynamics? A test of BORFOR and FORSKA2V in the boreal forests of western Canada

Introduction

Northern ecosystems are increasingly recognized as playing an important role in climate change (Woodwell et al., 1998). Boreal forests in particular have the potential to form an important biotic feedback. These forests store such large amounts of carbon, about 800 GtC (Apps et al., 1993), that relatively small changes can have substantial impacts on atmospheric carbon. For example, a carbon loss of just 0.1% per year from boreal forests, which is in line with the 0.8 GtC yr^{-1} loss postulated by Kasischke et al. (1995), would represent a 24% increase in the contemporary buildup rate of atmospheric carbon, estimated to be 3.3 GtC yr^{-1} (Schimel et al., 1996). Such a change could be expected to increase radiative forcing and affect climate change. At the same time, carbon storage in boreal forests is likely to be altered by a changing climate. Carbon pools are sensitive to climate, particularly temperature (Kauppi et al., 1997; Liski and Westman, 1997) and temperature increases in boreal regions are likely to be relatively large, according to projections of general circulation models (GCMs) (Kattenberg et al., 1996). The potential for climate change feedbacks is clear; however, their magnitude and sign remain uncertain.

Because of the long timescales involved with climate change, experimental data are difficult to acquire and assessments of impacts often rely on computer simulations. Patch models, also termed gap dynamics models, are frequently used for forest simulation because they can explicitly represent climatic and other abiotic variables, they can operate over scales of decades to centuries, and after 25 years of development, their strengths and limitations are relatively well understood (Bugmann, 2001b). In the boreal region, patch models have been widely used to predict the effect of changing climate on carbon storage and dynamics (Nisbet and Botkin, 1993; Karjalainen, 1996b; Karjalainen, 1996a; Sykes and Prentice, 1996b; Sykes and Prentice, 1996a; Pussinen et al., 1997; Price et al., 1999b), as well as species composition and biomass (Solomon, 1986; Pastor and Post, 1988; Overpeck et al., 1990; Kellomäki and Kolström, 1992; Post et al., 1992; Burton and Cumming, 1995; Post and Pastor, 1996; Price and Apps, 1996; He et al., 1999; Bugmann and Solomon, 2000; Ehman et al., 2002; He et al., 2002). They have also been used to study yield and productivity (Kellomäki and Kolström, 1993; Kellomäki and Kolström, 1994; Kellomäki, 1995; Beuker et al., 1996; Makipaa et al., 1998), stand structure (Lindner et al., 1997), frost damage (Kellomäki et al., 1995), regeneration (Kellomäki and Väisänen, 1995), and species ranges (Sykes and Prentice, 1995; Sykes, 2001) as well as for examining past climate changes (Solomon, 1985; Campbell and McAndrews, 1993; Cowling et al., 2001).

Despite the insights gained, validation of patch models remains problematic, particularly for abiotic variables. Validation methods are generally weak, relying on perceived realism, comparison of predicted wood volume against generalized growth and yield curves, comparisons of regional species compositions with that predicted for a typical site, and in some cases against site-specific biomass. The technique of validating a model for a region based on typical abiotic input variables is also questionable because it pre-supposes that it is known what the average values are for a region and assumes that the model responds linearly to each variable. Neither assumption is reasonable. Further, models are often applied without revalidation outside the region or range of conditions for which they were parameterized (e.g., Pastor and Post, 1988; Bradley et al., 1995; Nalder and Merriam, 1995; Yarie et al., 1995).

By their nature, patch models simulate specific sites, usually a plot or patch of about 0.1 ha. Consequently, any meaningful testing should be performed at the same scale. The model output may be taken to be representative of a larger area, but this generally implies that the site conditions within that area are completely homogeneous. Such an area is typically assumed to be a forest stand which is generally delineated by differences in soil, moisture regime, slope or aspect and disturbance history. Applying patch models to stands is attractive because this is the scale at which forest inventory data are maintained. Consequently, stand data may be used for validation of patch models, and there is increasing interest in applying the predictions from patch models at this spatial scale.

The validation problem is compounded by the large differences between regions within the boreal forest zone. Within the circumpolar boreal, there are wide ranges of temperatures, precipitation and soils, as well as distinct suites of species. Consequently, limiting factors are likely to vary from region to region. For instance, in western Canada there is strong evidence that moisture deficits limit the southern edge of the boreal forest (Hogg, 1994; Hogg and Schwarz, 1997), but in Scandinavia thermal limits and competition seem more important (Sykes and Prentice, 1995). The response of different regions, even to the same climate change signal, can therefore be expected to vary appreciably. To improve the confidence with which a model can be applied to a specific region, it is important to validate it for that region.

The Boreal West Ecoclimatic Province of Canada (Ecoregions Working Group of Canada, 1989; Siltanen et al., 1997), referred to hereafter as the western boreal, is a region formed by a 1000 km wide arc of continental boreal forest that stretches from the Ontario/Manitoba border west and north to the base of the western mountain chain in Alberta and Northwest Territories. This region appears particularly sensitive to climate change: it has undergone 1.3-1.7 °C warming over the last century (Environment Canada, 1992) and GCM projections indicate it will undergo greenhouse warming much greater than the global average in the future (Kattenberg et al., 1996). Yet relatively few studies have been carried out in this region and data from other boreal regions may not be applicable because conditions here are unique. It currently receives lower precipitation than Canada's eastern boreal while radiation regimes are quite different from interior Alaska to the west, because of its low relief and more southerly location. Compared with northern Scandinavia, the climate is drier, colder and more continental, and the suite of native species is different. Similar climatic conditions do exist in continental Siberia, but winters there tend to be colder and the different history of deglaciation has led to larch and pine being dominant over much of the landscape. Consequently, existing patch models, all of which have been developed and parameterized for other regions, would need testing before they could be applied with any confidence in the western boreal.

Tests were carried out with two patch models that have been widely used for simulation of boreal forests and that represent contrasting approaches. The first model was developed for interior Alaska (Bonan, 1989a; Bonan and Korzuhin, 1989; Bonan, 1990a), and has been termed BORFOR (Bradley et al., 1995). It has been tested at several North American sites outside its region of parameterisation and provided reasonable correspondence between a suite of predicted variables and those measured in stands (Bonan and Shugart, 1989; Bonan, 1990b). It also gives credible results when applied to tracts of boreal forests in Ontario (Nalder and Merriam, 1995) and the Amur region of eastern Russia (Bradley et al., 1995). The second model, FORSKA2, was developed and tested using site data from central Sweden (Prentice et al., 1993). It has been parameterized for North American species (Price et al., 1993) and used for climate change studies for a north-south transect of the boreal forest in western Canada (Price and Apps, 1996). More recently, Price et al. (1999a) modified it to better represent the effects of interannual climate variability; this version, termed FORSKA2V, has given good results in Western Canada (Bugmann et al., 2001) and is the version tested here.

Although both models are based on the gap dynamics paradigm from JABOWA (Botkin et al., 1972) and FORET (Shugart, 1984), there are substantial differences. Tree growth in BORFOR is calculated using the traditional tree growth equation (Botkin et al., 1972) which relates annual volume increment to leaf area and a factor (equal to 1 minus the product of diameter and height divided by the product of species-specific maximums of diameter and height) which crudely represents respiration. With tree height and leaf area defined in terms of diameter, the optimum annual diameter increment is calculated based on a species-specific growth constant, *G*, which defines the initial rate of growth of young trees. *G* is estimated by assuming that trees reach 2/3 of their maximum diameter at 1/2 their maximum age. The model also calculates moss growth and mortality, and simulates forest floor development as the balance between litter input and decomposition. Annual litter cohorts are tracked and decomposition is calculated from an empirical function relating percent decay to nitrogen content and soil thaw depth. Optimum annual tree growth is reduced by a number of scalars which take account of shading, growing degree days (GDD), soil thaw depth, low soil moisture and soil nitrogen availability. Solar radiation, soil thaw depth and soil moisture are calculated monthly and aggregated over the year or growing season to estimate site conditions. A generalized insolation routine calculates incident net solar radiation taking account of slope and aspect and direct and diffuse radiation. Soil thaw depth is calculated based on water content and heat sums using Stephan's degree-day formulae. Soil moisture of each layer is estimated using a tipping bucket approach with inputs from precipitation and outputs from AET, soil thawing and drainage. Potential evapotranspiration (PET) is calculated from a modified Priestley-Taylor formulation. Trees saplings are established until leaf area is at least 20% of the plot area with a small number per year thereafter; saplings are drawn from each species present with a probability related to the scalars that limit growth as well as other factors such as seed availability and moss cover. Apart from disturbances (fire or insect attack) tree mortality is a function of potential longevity (only 1% of trees reach maximum age) and stress as measured by dbh increment falling below a predefined threshold (1% probability of surviving 10 years of stress).

FORSKA2V differs from BORFOR in a number of important ways. First, the traditional tree growth formulation is replaced by a more physiologically-based function that relates daily assimilation to photosynthetically active radiation (PAR), leaf area, a species-specific maximum net assimilation rate constant and an environmental scalar, and relates daily respiration to sapwood volume, air temperature and a respiration constant; net assimilation is reduced by a further scalar to represent nutrient limitations. Second, tree structure is improved by representing the crown as a cylinder rather than a disc. Third, the traditional GDD parabola scalar is replaced by a daily parabolic response to temperature that is summed over the growing season. Fourth, soil moisture is estimated on a daily basis with AET being the minimum of supply and demand, PET calculated using the Priestly-Taylor formulation, and drought stress related to the sum of soil water potential over the growing season. Fifth, FORSKA includes switches for growth and regeneration to capture winter chilling and summer warmth requirements for some species. Sixth, tree mortality is a function of growth efficiency (stem volume increment divided by leaf area) rather than age and dbh increment. Sixth, establishment is a Poisson function with an expected value defined by a species-specific optimum rate modified by a scalar for environmental conditions; establishment rates are increased in the year after fire. Finally, FORSKA2V does not simulate moss or forest floor layers.

The objective of this study was to evaluate BORFOR and FORSKA2V as previously parameterized and validated for simulation of stand dynamics in the western boreal by testing their predictive power for a range of stand ages and abiotic variables. The study was limited to upland stands dominated by *Populus tremuloides* Michx. (trembling aspen) and *Pinus banksiana* Lamb. (jack pine). These species together account for 50% of timber volume in the western boreal (calculated from data in Gray, 1995) and dominate upland areas. Mixed stands are common in the western boreal, but the intention here was to test the models under the simplest possible conditions. The approach, recommended by Bugmann et al. (2001), is to develop chronosequences by surveying stands across a range of ages then to simulate each stand and compare the output of each model with observed chronosequence data. Chronosequences are developed for each species in each of three contrasting climatic zones.

Methods

Observed stands

Upland forest stands were sampled in three distinct climatic zones (Figure 5-1). These zones were chosen to provide contrasting extremes of temperature and precipitation within the western boreal. Stands were selected within or close to the Southern Study Area of the BOReal Ecosystem-Atmosphere Study (BOREAS) (Sellers et al., 1997) near Prince Albert, Saskatchewan (Zone 1), in Wood Buffalo National Park near Fort Smith (Zone 2), and near the BOREAS Northern Study Area (NSA) centred on Thompson, Manitoba (Zone 3). These zones represent warm-dry, cold-dry and cold-moist conditions respectively.

Within each climatic zone stands of various ages (time since stand-replacing fire) were sampled that were dominated by *P. banksiana* or *P. tremuloides* to provide a chronosequence of at least 10 stands for each species and zone. Stand ages were determined from increment cores, fire scars and fire history records where available. Latitude, longitude, elevation, slope and aspect were measured for each stand and tree cover was determined using fixed area plots. In each plot, the species, height, diameter at breast height (dbh) for each live and dead tree was measured, and biomass calculated using allometric equations of Evert (1985). Using a specially designed corer (Nalder and Wein, 1998a), 10 soil cores were taken and measurements were taken of forest floor organic matter using loss-on-ignition, forest floor depth and bulk density, and moss/lichen biomass. For the underlying mineral soil, depth to impermeable layer was measured if less than 1 m. For the upper 20 cm, field determinations of texture were made, organic matter content was determined using loss-on-ignition, and bulk density was calculated using the relationships of Grigal (1989). Gravimetric moisture contents at saturation, field capacity and wilting point were also measured using a pressure plate apparatus, and converted to a volumetric basis using the derived bulk densities. Sampling and measurements are described in more detail in Nalder and Wein (1999).

To assess the dynamics of each stand chronosequence, regressions of live tree biomass and stem density were performed against stand age. For each variable, several regression models were examined, and the one giving the highest significance level for all chronosequences while providing realistic patterns over a 150 year period was chosen.

For each stand, climatic variables were estimated by spatially interpolating from surrounding climate stations using the "Gradient-plus-Inverse Distance Squared" (GIDS) technique (Nalder and Wein, 1998b) and 1951-1980 Normals (Environment Canada, 1982; Environment Canada, 1983). Climatic variables were hours of bright sunshine, mean and standard deviation of monthly temperature and precipitation, and maximum and minimum monthly temperature. Cloudiness (tenths) for each month was calculated as:

$$\text{Cloudiness} = 10(1 - H_{bs}/H_{dl}) \qquad (1)$$

where H_{bs} and H_{dl} are mean total monthly hours of bright sunshine and of daylight, respectively.

Stand simulations

Each of the 80 stands was simulated with both models. Each model was modified to prescribe disturbances, to generate a stochastic climate and to track standing dead trees (details follow), but were otherwise unchanged. BORFOR is described by Bonan (1990a; 1990b) and FORSKA2V by Price et al (1999a), Price et al. (1993) and Prentice et al. (1993).

For BORFOR, species parameters and moss productivity were taken from Bonan (1989b) and litter and fire effect parameters from Bonan (1990a). Site-specific input variables were latitude, longitude, elevation, slope and aspect, as well as mineral soil depth, texture and volumetric water holding capacities (SAT, FC, WP). An initial forest floor nitrogen content of 0.008 g g^{-1} was assumed. Climatic and initialisation variables are described in subsequent paragraphs. Each run simulated 30 patches each of 0.083 ha. For FORSKA2V, species parameters were taken from Price et al. (1999a). The only site specific inputs were latitude and volumetric available water holding capacity (AWHC) derived from stand data. The model was run for 200 patches each of 0.1 ha. Both models were run with only the dominant species present following Bonan (1990b), i.e., either *P. banksiana* or *P. tremuloides*. This assumes that the sampled stands regenerated from similar mono-specific stands where regeneration sources for other species were absent.

Initial conditions for each simulation run are set differently in each model. BORFOR was initialized by assuming tree and forest floor biomass typical of a 75-year old stand (from Nalder and Wein, 1999) and applying a high intensity and severity fire as per Bonan (1990b). For FORSKA2V, initialisation was performed by running for two 75-year cycles, with each cycle terminated with a disturbance. Although there was no information on conditions in the sampled stand prior to the stand-originating fire, it seemed reasonable to assume an age of 75 years, since this is typical of reported fire recurrence intervals in the western boreal (Van Wagner, 1978; Johnson, 1981; Viereck, 1983; Murphy, 1985; Johnson, 1992; Heathcott and Cornelsen, 1994; Larsen and MacDonald, 1995; Larsen, 1997; Weir and Johnson, 1998). In any case, the outputs were not sensitive to this assumption. After initialisation, both models were run without disturbance for a further 150 years to simulate the development of each stand. Seeds for the random number generator in each model were randomly selected for each run.

Both models were run with a variable climate following Bonan and Shugart (1989) and Price et al. (1999a). For each stand, a stochastic climate record for monthly temperature and precipitation was generated using the spatially interpolated monthly means and standard deviations. Monthly temperature was assumed to be normally distributed. For monthly precipitation, a two parameter gamma distribution was used (Bratley et al., 1983). The shape and scaling parameters for the gamma distribution were:

$$\alpha = k \times \sqrt{\mu_P / \sigma_P} \quad \text{and} \quad \beta = \mu_P / \alpha \quad \text{.........} (2)$$

where μ_P and σ_P are the mean and standard deviation, respectively, of monthly precipitation, and k is an empirically-derived multiplier described in the following paragraph. Given the lack of variability data for cloudiness, as well as the imprecision of estimates of cloudiness, it was not worthwhile trying to generate a stochastic cloudiness. Consequently, mean monthly cloudiness was used for all simulations.

Forest models can be sensitive to interannual variations (Lindner et al., 1996; Bugmann and Cramer, 1998; Kangas, 1998; Hogg, 1999; Price et al., 1999a). To check for realism of the stochastic time series, temperature and precipitation series were generated for each month using a climate station within the region of interest that had a long period of record (Fort Smith). As a result of these tests, it was necessary to adjust the gamma distribution by means of a shape factor multiplier, which was set to a value of 1.7, and to truncate the output at 4 times the mean (μ_P) to avoid unrealistically high precipitation events. These climate generation routines were tested by generating stochastic climate for a further three climate stations with long period-of-record data (Fort Simpson, Fort Vermilion and Waseca) and checked for realism in three ways: 1) comparison of mean and standard deviation for the stochastically generated time-series with those of the original data set used to generate the distributions, 2) visual comparison of the year-to-year patterns of variability of the stochastic series (plotted as a time series) with the original period-of-record data, 3) visual comparison of the distributions of the stochastic series (plotted as histograms) with the original period-of-record data.

Model tests

Given the stochastic processes in each model, runs with differing seeds for the random number generators give different results. To assess this variability, 30 runs were carried out with each model, using different seeds for each run, for both stochastic climate and constant climate and for both a typical *P. banksiana* stand and a typical *P. tremuloides* stand, i.e., a total of 120 runs with each run simulating 30 patches (BORFOR) or 200 patches (FORSKA2V). For each set of 30 runs, coefficients of variation (CV) were calculated for tree biomass and stem density at 10-year intervals.

To test the predictive power of each model, observed values of several variables were compared against the simulated values for those variables at the age equal to that of the stand being simulated. Variables compared for both models were live tree biomass, standing dead tree (snag) biomass and stem density. For BORFOR observed versus predicted values were also compared for moss/lichen biomass and forest floor organic matter. For each variable, the relationship between observed and predicted values was tested by linear regression. Neither model tracks snags, so for comparison with observed data each model was modified to calculate snag biomass in each year. For this purpose, it was assumed there was a linear breakdown of snags as a function of time with half-lives of 5 and 10 years for *P. tremuloides* and *P. banksiana*, respectively. This assumption is believed to be reasonable based on data from a study in progress. Lee (1998) shows half-lives of 15-20 years for *P. tremuloides* in Alberta, but this is for relatively mature stands where snags are more protected from wind.

The ability of each model to replicate stand dynamics was tested by comparing the observed dynamics for each of the six chronosequences (i.e., two species in each of three climatic zones) with those from model runs for two variables, live tree biomass and stem density. Given that there is some variation in site characteristics within a chronosequence (Table 5-1), the site-specific input variables for each model run, including climate, were set to the observed averages from all stands in that chronosequence. Because of the high stochasticity of each model (see Results and Discussion section) ten runs were performed for each chronosequence, each with random seeds, and outputs were averaged. Observed dynamics were estimated from regression equations of live tree biomass and stem density against stand age.

Discrepancies between observed and predicted data were investigated to determine the likely reasons and identify possible improvements. Model runs were repeated with altered parameters to test for improvements.

Results and Discussion

Chronosequence characteristics

Characteristics of the six chronosequences are summarized in Table 5-1. Live tree biomass showed strong and linear increases with time, ranging from 94-196 g m^{-2} yr^{-1}, and being highest for *P. tremuloides* in all zones. Zone 1 had the highest accumulation rates for both species, with little difference between zones 2 and 3. There was no evidence in any of the chronosequences of an upper asymptote, i.e., linear models gave better fits than logarithmic or polynomial models in all cases (Nalder and Wein, 1999). For tree density, linear, logarithmic, quadratic and cubic models gave unrealistic patterns outside of the chronosequence range and were discarded. Power, inverse and exponential models gave very similar r^2 values: a power model was selected as it gave a more consistent and realistic pattern across all chronosequences, and because tree density is recognized as a power function of biomass (Westoby, 1984), which as noted above, was linearly related to age.

Stochastic climate realism

Three test stations provided fairly complete long-term data, Fort Vermilion (76 years), Fort Simpson (95 years) and Waseca (85 years). A total of 72 series (3 stations x 2 variables x 12 months) were compared against stochastic series. As expected, the stochastic series reproduced the input means and standard deviations. Of more concern was the ability to reproduce frequency and duration of extremes, because both models proved quite sensitive to such extremes (see Predictive Ability section). For all 72 comparisons, the year-to-year patterns and distributions for the stochastic series were consistent with the period-of-record data. This is illustrated by Figure 5-2 which shows one of the comparisons. There was no evidence that the frequency and magnitude of extremes, or the likelihood of two or more years with low values, were misrepresented by the stochastic series. In this sense, the stochastic series seem to provide a good approximation to real climate. There are, however, some caveats.

First, no attempt was made to reproduce auto-correlative or cross-correlative characteristics of observed climate series. Although such correlations are important with daily data (Richardson, 1981), the correlation coefficients were comparatively low with monthly data. Consequently, it is doubtful whether inclusion would markedly improve the realism of the stochastic series. Second, the stochastic series do not replicate decadal-scale trends, which were evident in some of the observed data, and also provide different timings of the extremes. Both may affect the simulated development of stands, e.g., a prolonged cool period or a drought year may have more effect on a regenerating stand than on a mature stand.

Model Stochasticity

Both models were sensitive to the differing stochastic climate realisations generated by different random number generator seeds (Figure 5-3). The run-to-run CV's for tree biomass with stochastic climate (Figure 5-3) depend upon the model, the simulation year and the conditions being simulated, but are generally high, up to about 20% for BORFOR and about 80% for FORSKA2V. Results for tree density were similar. It should be noted that not all of this variability is due to climate since the seeds for the random number generators also affect the establishment and mortality routines. Even with constant climate (Figure 5-3), variability in predicted biomass and stand density is not trivial, but stochastic climate is generally the major contributor. Whether stands are this sensitive to climate in reality is an open question. Examination of individual runs showed that the high variability was mainly due to instances of high mortality. Although infrequent, these greatly affected the trajectory of biomass, a problem discussed further in the following section.

Given the climate sensitivity of the two patch models, it would obviously be preferable to utilize observed climate data. This is not possible in the western boreal, however, because too few climate stations have long-term records. Consequently the simulations must be approximations of actual stand development. Despite this, some fundamental weaknesses in each model were evident.

Predictive ability

Figure 5-4 plots observed values of five variables against those predicted by BORFOR and FORSKA2V. It should be noted that FORSKA2V does not provide predictions of forest floor or the moss/lichen layers. Although it was expected that points would generally cluster along the 1:1 line shown on each plot, e.g., see Figure 1 of Makipaa et al. (1998), this did not occur in any instance. R-square values were less than 0.15 for linear regressions of observed against predicted, except in the case of live tree biomass for FORSKA2V ($r^2 = 0.33$). In this case, the slope of the regression line was 0.49, indicating consistent underestimates of biomass: three points gave values close to observed, all mature stands with high biomass, suggesting that underestimates were occurring mainly in young stands. The lack of predictive ability of both models in this study area is remarkable.

Predictions of dead tree, forest floor and moss biomass are dependent on correct representation of live trees. Given the poor prediction for live tree biomass and stem density, it is not surprising that these three variables were inaccurately simulated. Consequently, these variables are not considered further in this chapter.

It is possible that the poor predictive ability of the models arises from their inherent stochasticity in conjunction with the variability inherent in field sampling. For example, replicated simulation runs of BORFOR gave CV's for live tree biomass of up to about 20% (Figure 5-3) while the means of observed live tree biomass had relative standard errors that averaged 14%. Obviously, there is ample scope for the predicted not coinciding with the observed, even if the model was a perfect representation of reality. Can these sources of variability, however, account for the poor predictive power? To answer this question, 80 values randomly distributed between 0 and 250 were generated, representing true values of tree biomass. To generate an "observed" series each point was randomly sampled assuming a normal distribution with a mean equal to the "true value" and a standard deviation equal to 15% of the mean. A "predicted series" was generated in the same way but with a CV of 20%. Linear regressions of the predicted series against the observed series produced an r^2 of about 0.8 and a slope close to one. The results were similar for stem density. Clearly, variability in sampling and simulation can only account for a small part of the discrepancy between observed and predicted.

A clue to the lack of predictive ability can be gained by examining the extreme cases. Sixteen of the BORFOR simulated stands and 32 of the FORSKA2V simulated stands gave extremely low biomass (Figure 5-4). When the simulation outputs were examined for these stands, biomass was low regardless of age and this in turn was due to frequent instances of high mortality.

For BORFOR, the high mortality occurred with *P. banksiana* stands in zones 2 and 3, and was principally due to the growing season growth multiplier, which was frequently at or close to zero. The consequent low growth gave high stress-induced mortality when it occurred in successive years and the stands remained in a perpetual state of regeneration rather than reaching maturity. Clearly this was unrealistic. It was, however, a direct consequence of the minimum GDD parameter, which was set to 830 degree days as per Bonan (1989b). Given the parabolic growth function of the model, GDD values close to 830 gave a growth multiplier equal to or close to zero. Yet along the northern peripheries of Zones 2 and 3, GDD values calculated by BORFOR from the stochastically generated climates, as well as from observed period-of-record data, were frequently lower than 830. The GDD parameterisation would appear to be in error.

The parabolic response function that relates the growing season growth multiplier to GDD has a very steep slope close to range limits, and therefore patch models using this formulation can be very sensitive to choice of GDD_{min} and GDD_{max} (Botkin and Nisbet, 1992). Consequently, assessment of the range limits is critical. However, estimates of GDD_{min} and GDD_{max} from different studies vary by up to 722 GDD (Table 5-2). Obviously, not all can be "correct". Much of the variation in estimates undoubtedly comes from the subjectivity inherent in the traditional method of determining these parameters, which is visually overlaying published GDD maps on species range maps. There are, however, further difficulties. Models generally calculate GDD differently to the methods used by compilers of GDD maps. Many gap models, including BORFOR, base site estimates of GDD on monthly mean temperature (T_m), but published GDD isoline maps are usually based on daily mean temperatures (T_d). Values derived from monthly means are lower than those based on daily means (to understand this, consider a hypothetical month where T_d increases linearly from 2 to 8 °C over the month giving T_m=5 °C; using a base temperature of 5 °C, this month would accumulate zero GDD based on T_m, but would accumulate 21 GDD based on T_d). In the study region, it was found that GDD calculated from T_m underestimated published GDD (Environment Canada, 1994), typically by 5-10%. GDD may also be underestimated by choice of the wrong base temperature, e.g., for stands used in this study, a base temperature of 5.56 °C (42°F) underestimated GDD by about 50 GDD compared with a base temperature of 5 °C. These differences, though not large, can be critical in regions close to the simulated limits of a species range. Consequently, GDD parameters may need to be re-estimated (Fischlin et al., 1995).

To provide a more objective and more accurate method of estimating GDD range limits, while avoiding biases due to incomparable GDD estimates, a new procedure was developed. North American range maps were digitized for both species (Burns and Honkala, 1990), and for each digitized point GDD was calculated as $\Sigma\{d*(\max(T_m-5,0))\}$ where T_m is mean monthly temperature for the period 1951-1980 and d is the number of days in the month. T_m was estimated by spatially interpolating from the nearest 25 climate stations in the Global Historical Climatology Network (GHCN) database (Peterson and Vose, 1997). Only stations with at least 15 years of data during the period 1951-1980 were used in calculating T_m. The GIDS method (Nalder and Wein, 1998b) was used for interpolation, using latitude, longitude and elevation as predictors. Elevations were taken from the GHCN database for climate stations, and from a global digital elevation model (DEM) (NOAA/NGDC, 1992) for each digitized point. The minimum and maximum of the calculated GDD values assigned to each digitized point defined the appropriate species parameter. No attempt was made to digitize range limits in mountainous areas as the scale of the range maps and resolution of the DEM (5 minutes) made it impossible to capture altitudinal gradients.

For BORFOR, this new procedure gave very different values to those previously used (Table 5-2), particularly for minimum GDD: the value for *P. banksiana* dropped from 830 to 438, and for *P. tremuloides* from 280 to 158. Maximum GDD values increased slightly in both cases. To test the effect of the new parameters, BORFOR was re-run for the 80 stands. This time, only 3 stands suffered high mortality events, a considerable improvement on the 16 noted previously. Nevertheless, the relationship between observed and predicted was still poor (r^2 for stem density increased from 0.12 to 0.31; but r^2 for live tree biomass decreased from 0.10 to 0.02) indicating problems other than the GDD parameters (see Dynamics section). It should be noted that the difficulties outlined here with estimating GDD parameters tend to reinforce previous criticisms of the parabolic GDD response function (Prentice et al., 1991; Bonan and Sirois, 1992; Botkin, 1993; Sirois et al., 1994; Sykes and Prentice, 1995; Loehle and LeBlanc, 1996; Schenk, 1996; Bugmann, 2001a; Lexer and Honninger, 2001)

For FORSKA2V, the high mortality phenomenon occurred with both species in all zones. The frequent high mortality events occurred because the drought growth multiplier dropped to zero many times over the 150 years of the simulation. Whenever this occurred, the combined multiplier became zero, causing growth and therefore realized growth efficiency to also drop to zero. This in turn caused all trees to be subject to a high stress-induced probability of mortality (38%) in those years when summer precipitation was relatively low. For *P. banksiana*, Larsen and MacDonald (1995) report that growth is positively correlated with summer precipitation, suggesting that drought can be an important control on growth, at least for *P. banksiana*. In this sense the model is realistic. Clearly it is overly sensitive, however, because there was no evidence in the observed stands of frequent high mortality events. A similar over-sensitivity to drought has been reported for ForClim in Switzerland (Fischlin et al., 1995) and ForClim and BOREALIS in western Canada (Bugmann et al., 2001).

FORSKA2V was originally designed for (humid) maritime climates (Prentice et al., 1993), and it was found necessary to revise the water balance model in FORSKA2V for application in the western Canadian boreal (Price et al., 1999a; Bugmann et al., 2001). The selected parameters provided an improved landscape distribution of species, but clearly need refinement for site-specific simulations. The over-sensitivity to drought could be a result of drought tolerance parameters being set too low and/or due to the steep slope of the function that relates seasonal soil water deficit to drought growth multiplier (see Figure 1 of Price et al., 1999a). There are, however, other possibilities. First, the core model in FORSKA2V can be set to update patches at timesteps greater than one year. Using a timestep of 2 years (as per Prentice et al., 1993), buffers trees against mortality from a single climatically unfavourable year, and may minimize the high mortality events simulated here. Second, measurement of available water holding capacity (AWHC) is not a precise science, and it may be that some data underestimate true field water holding capacities. Third, the use of a single AWHC value for all patches is probably unrealistic because of spatial variability in soil conditions within a stand. A more realistic method, which would tend to avoid the high mortality events noted above, would be to define AWHC values for each patch based on an observed mean and standard deviation. This approach was suggested by Price and Apps (1993). It is beyond the scope of this paper to resolve these issues, but clearly further work is required to parameterize and validate FORSKA2V drought formulations for the western boreal.

Dynamics

Further insight into the lack of predictive ability of both models can be obtained from a comparison of their dynamics against observed patterns (Figure 5-5). Both models gave very different patterns to those observed.

Two of the six chronosequences simulated by BORFOR, *P. banksiana* in Zones 2 and 3, gave unrealistically low peak values of biomass because of the problem with the growing season growth multipliers discussed previously. The four remaining chronosequences show a consistent pattern: the model accumulates biomass too rapidly, then goes into a protracted decline while observed biomass is still increasing (Figure 5-5a). The simulated peaks are also generally much lower than the observed maxima. It should be noted that the simulated and observed curves cross between 60 and 90 years. This provides a clue to the success of the previous validations (Bonan and Shugart, 1989; Bonan, 1990b), because these were mostly carried out on mature stands. For instance, the tree biomass of 70-year old stands dominated by *P. banksiana* and *P. tremuloides* in northern Minnesota was simulated within 19 and 2 %, respectively (Bonan and Shugart, 1989). For the single test of younger stands (13 to 57-year old *P. banksiana* in New Brunswick), the range of simulated biomass values was considerably higher than observed (Bonan, 1990b).

The high initial biomass accumulation rates of BORFOR are mainly a consequence of the high optimum growth rates, which are defined by the fundamental growth equation (Botkin et al., 1972; Botkin and Nisbet, 1992) and the assumption that trees reach $\frac{2}{3}$ of their maximum dbh at $\frac{1}{2}$ their maximum age. This formulation has been common to most gap models since JABOWA, but it was early recognized as an arbitrary assumption that can lead to unreasonable growth rates (Botkin et al., 1972). The assumption is used to solve the growth equation to obtain a value for a species-specific assimilation rate factor, *G* (Botkin et al., 1972); the effect of different assumptions is shown by Botkin (1993). To provide realistic *G* values for a range of species in the Great Lakes region of the United States, Botkin and Nisbet (1992) modified this assumption so that the ratio of dbh/dbhmax at $\frac{1}{2}$ maximum age varied among species from 2/9 to 8/9. Given this background, it seemed likely that for *P. banksiana* and *P. tremuloides* the value of *G* calculated from the "$\frac{2}{3}$ maximum dbh at $\frac{1}{2}$ maximum age" assumption was unrealistically high. This hypothesis was tested for *P.banksiana* in Zone 1. Biomass accumulation rates were comparable to that observed when *G* was set to 20% of its original value, but maximum biomass was reached at about 60 years and thereafter declined. To achieve realistic growth for the full span of the chronosequence, it was necessary to reduce age-dependent mortality and critical diameter increment for stress mortality to 10% of their original values. Undoubtedly there are other combinations, or changes to other parameters such as maximum age, that would produce similar results. It is probably possible to re-parameterize the model to produce reasonable agreement with the observed chronosequences. However, it seems that the need for such large changes in parameters raises crucial questions about the underlying assumptions used to set these parameters. Possibly, the conventional gap model growth formulation and assumptions are not suitable for simulating the dynamics of boreal stands, at least within the western boreal of Canada.

BORFOR also seriously underestimated stem density in all chronosequences (Figure 5-5b). Part of this underestimation is due the model limitation of 700 trees per patch, which imposes a maximum stem density of 700/0.0833=8400 stems ha^{-1}. This limitation is common to nearly all patch or gap models developed since JABOWA, but is inappropriate for replicating the early stages of stand development for *P. banksiana* and *P. tremuloides*. Initial densities after fire are in the order of 10^5 stems ha^{-1} (Carroll and Bliss, 1982; Peterson and Peterson, 1992), and based on observed dynamics in Figure 5-5b, stem densities are greater than 8400 stems ha^{-1} for the first 30-40 years of stand development. Given an average stand age of 75 years, this implies that gap models such as BORFOR are incapable of replicating stand structure for at least half of the stand life.

It should be noted that 700 trees per patch is not an inherent limitation of either model, but rather a practical limit: with both models, small increases caused array overflows. It may be possible to modify the models to handle the required initial densities, but this would greatly increase the processing time of simulations.

There is a further problem with the simulation of stand density. Even though BORFOR starts with unrealistically low stem densities, it thins aggressively over the first 30-40 years, so that observed and simulated curves do not intersect until about 100 years, if at all. This behaviour is a consequence of the rapid growth of individual trees in the model which creates intense competition for light and consequent high mortality of less vigorous individuals due to low light. In contrast, the chronosequnce data suggest a more appropriate model for these species would be one in which high densities would emphasize suppressed growth rather than high mortality.

The formulation of tree growth in FORSKA2V is completely different and not surprisingly it predicted quite different dynamics from BORFOR, although still far removed from observed patterns (Figure 5-5). Biomass was seriously underestimated in all chronosequences. Stem density was a small fraction of observed, only approaching observed values for very old stands, and was never greater than one tenth of the 700 trees per patch limitation mentioned above. Clearly there was a problem with the regeneration routine. In the original FORSKA2 model, regeneration was simulated as a Poisson process defined by a species-specific optimum rate reduced by several growth and regeneration multipliers. This fails to capture the pulse of regeneration that occurs after fire with some species. Price et al. (1999a) attempted to remedy this deficiency in FORSKA2V by increasing the rate significantly, but only during the year after disturbance. For the chronosequence runs, establishment rates for *P. banksiana* were about 7 saplings ha^{-1} with first year rates of 29-42, and for *P. tremuloides* about 3 saplings ha^{-1} with first year rates of 14-18. The long-term rates may be realistic (it has been observed that regeneration after the first year is very low until stand breakup) but the initial establishment is still orders of magnitude less than the 10^5 stems ha^{-1} rate noted in the previous paragraph. This leads to much lower stem densities than those observed in the chronosequences. It is concluded that the FORSKA2V regeneration routines are inappropriate for fire regeneration of *P. banksiana* and *P. tremuloides* in the western boreal.

The unrealistically low regeneration appears to be the primary cause of the generally low estimates of biomass, i.e., growth rates of individual trees may be reasonable, but there are too few trees on each patch to give observed biomass values. To test this hypothesis, the regeneration routine was over-ridden for the first year after disturbance and 7000 stem ha^{-1} were established, corresponding to the model limitation of 700 trees per patch. Although stem density is still underestimated during the first few decades, the pattern of biomass accumulation was much closer to that observed for all chronosequences. The slope of the regression line for observed versus predicted biomass increased from 0.30 to 0.60 for *P. banksiana* and from 0.54 to 1.35 for *P. tremuloides*. It should be noted that growth rates are very sensitive to the species-specific growth constant and that for *P. tremuloides* this parameter had previously been tuned to improve species biomass and composition along a transect of the western Canadian boreal forest (Price et al., 1993). It is likely that this adjustment was compensating for slow regeneration, and thus causes an overestimate of biomass when regeneration is forced to more realistic values. Clearly, representation of regeneration for *P. banksiana* and *P. tremuloides* is an important area to address with FORSKA2V.

Both models suffer from a further limitation in representing dynamics correctly because saplings are "planted" with a dbh of about 1.3 cm. This ignores the time that trees take to reach breast height, which can be many years in the western boreal, e.g., forest inventory surveys in Alberta suggest times of 10 and 5 years for pine and deciduous species, respectively (Alberta Environmental Protection, 1994). Part of the explanation for the success of patch models in other ecosystems may be that high initial regeneration rates have little effect on the stand dynamics if most of the seedlings die before reaching significant size. But for those species where mortality due to early competition is relatively low (notably boreal forest species such as jack pine), the model's failure to allow these high densities to persist could clearly affect the realism of the simulation. This represents another area that would need to be addressed to achieve credible simulations of stand dynamics.

The inability of these models to replicate dynamics of even the simplest boreal stands casts doubt on their predictive value when applied at regional scales. Regional studies may have given realistic biomass values (e.g., Price et al., 1999a), but if the models cannot replicate stand dynamics, they may be right for the wrong reasons. For example, the assumption made in many regional simulations that all species are present and competing for resources on each patch is clearly false, at least in the western boreal of Canada, where stands are often mono-specific and few have more than three species. As a general conclusion, the value of these models for conditions other than those for which they were parameterized is questionable, and the results of regional simulations (Bradley et al., 1995; Nalder and Merriam, 1995; Price and Apps, 1996; Price et al., 1999b) should be viewed with caution.

Conclusions

It is concluded that both models as formulated in previous studies are inappropriate for investigating stand level dynamics in the western boreal of Canada, at least for the two species examined here. A number of problems have been identified:

- BORFOR proved incapable of reproducing observed tree biomass dynamics. To obtain realistic patterns, optimum growth rates and mortality probabilities would have to be substantially reduced, i.e., extensive re-parameterisation would be required. It is difficult, however, to identify an objective rationale for altering multiple parameters and therefore it is suspected that this would be an unproductive exercise. Moss and forest floor dynamics were also unrealistic, but this is most likely a consequence of the unrealistic representation of tree growth.

- Both models grossly underestimated the stem densities of regenerating stands. In BORFOR, low stem densities were due an arbitrary limitation of 700 trees per patch combined with the unrealistically high tree growth rates mentioned above which forced rapid self thinning. In FORSKA2V, the regeneration routine, which is based on "planting" a few saplings per year, did not emulate the pulse of post-fire regeneration that occurs with *P. banksiana* and *P. tremuloides*.

- As a result of the extremely low stem densities, FORKSA2V considerably underestimated biomass over many decades. This should be correctable with a more realistic regeneration routine combined with adjustments to the species-specific growth parameter.

- GDD parameters for both models are suspect. A new method for estimating these parameters has been developed, which is believed to be more realistic, but the adequacy of the new parameters remains to be tested.

- Both models proved overly sensitive to climate extremes, which resulted in virtually no growth in many simulated stands. BORFOR was overly sensitive to cold summers, primarily due to unrealistic GDD parameterisation. In contrast, FORSKA2V was very sensitive to drought.

This study represents a preliminary step in developing a suitable model for simulating carbon dynamics in the western boreal forests. Each of the models investigated here has strengths and weaknesses. The tree growth routines of FORSKA2V were formulated to overcome the deficiencies of the conventional gap model approach, and it appears to offer more promise for replicating observed dynamics. It may be limited, however, because it does not simulate nutrient cycling and soil thermal regimes which are recognized as forming important controls on tree growth. Nor does it simulate the forest floor and moss layers, which affect soil thermal and moisture regimes and can represent substantial carbon pools. It is precisely these areas that BORFOR addresses, but further work needs to be done on BORFOR's tree growth routines to achieve realistic dynamics.

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Tables

Table 5-1. Characteristics of the six chronosequences (means are shown with standard deviations).

	P. banksiana			*P tremuloides*		
	Zone 1	Zone 2	Zone 3	Zone 1	Zone 2	Zone 3
No. of stands	14	10	12	17	17	11
Min. and max. age (yrs)	16-111	16-135	30-82	36-132	14-149	28-112
Species dominance (%)	99±3	100±1	93±6	93±8	93±10	98±3
Mean annual temperature (°C)	-0.7±0.2	-3.2±0.3	-3.9±0.5	-0.2±0.4	-3.0±0.3	-3.3±0.5
Annual precipitation (mm)	491±17	387±18	508±21	471±19	385±20	503±14
Mineral soil						
Bulk density (Mg m^{-3})	1.39±0.06	1.29±0.10	1.33±0.08	1.27±0.18	1.09±0.21	0.97±0.07
Available WHC (volumetric)	8%±3%	9%±5%	10%±5%	9%±4%	17%±5%	14%±6%
No. of stands in each texture class[a]	14-0-0-0	10-0-0-0	12-0-0-0	1-10-4-2	5-10-1-1	0-0-1-10
Regression of live tree biomass against stand age (linear model)						
Coefficient (g m^{-2} yr^{-1})	134	101	94	196	129	138
r-square	0.47	0.74	0.47	0.53	0.80	0.81
Regression of stand density against stand age (power model[b])						
b_0 (constant)	4.69E+5	6.10E+7	1.01E+6	4.70E+4	2.32E+5	7.90E+5
b_1 (coefficient)	-1.21	-2.21	-1.32	-0.71	-0.95	-1.27
r-square	0.81	0.95	0.43	0.20	0.62	0.67

[a] Soil texture classes are Coarse (S/LS), Medium (SL/L/SiL/Si), Moderately Fine (SCL/CL/SiCL) and Fine (SC/C/SiC) (Brady, 1990)

[b] DENSITY (stems ha^{-1}) = b_0 * AGE ^{b1}

Table 5-2. Minimum and maximum GDD parameters used in some patch models

Model	GDD minimum		GDD maximum	
	P. banksiana	*P. tremuloides*	*P. banksiana*	*P. tremuloides*
BORFOR[1]	830	280	2216	2461
FORENA[2]	830	743	2216	2461
JABOWA II[3]	639	333	2222	3101
FORSKA II[4]	600	400	NA	NA
FORET[5]	600	800	1500	2500
This study	438	158	2574	3275

Model references are: [1] Bonan (1990b), [2] Solomon et al. (1984), [3] Botkin (1993), [4] Price et al. (1993), [5] El-Bayoumi et al. (1984)

Figures

Figure 5-1. Western Canada showing location of the three climatic zones in which stands were sampled.

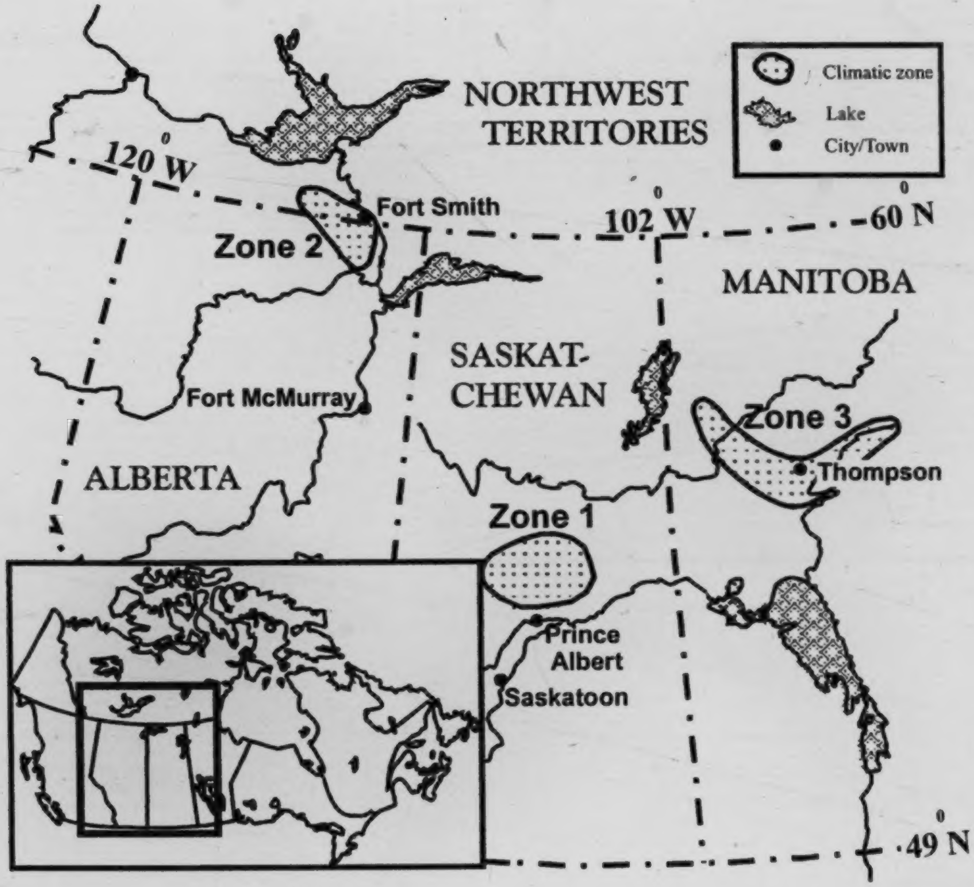
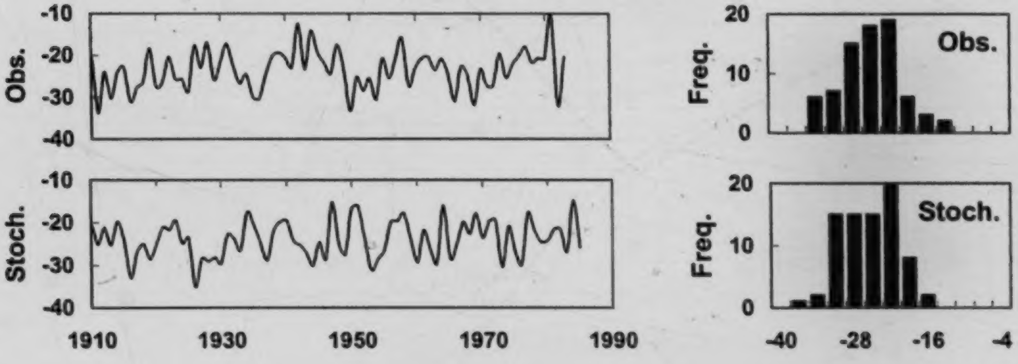

Climatic zone
Lake
City/Town
NORTHWEST TERRITORIES
120° W
102° W
60° N
49° N
Fort Smith
Zone 2
Zone 3
Zone 1
MANITOBA
SASKATCHEWAN
ALBERTA
Fort McMurray
Thompson
Prince Albert
Saskatoon

Figure 5-2. Example of a comparison of observed (Obs) period-of-record monthly mean climate data for January at Fort Vermilion with a stochastically generated series (Stoch) based on observed means and standard deviations. Generation of the stochastic series is described in the text. Time series are shown on the left, and distribution histograms on the right.

(a) January temperature (°C)



(b) January precipitation (mm)

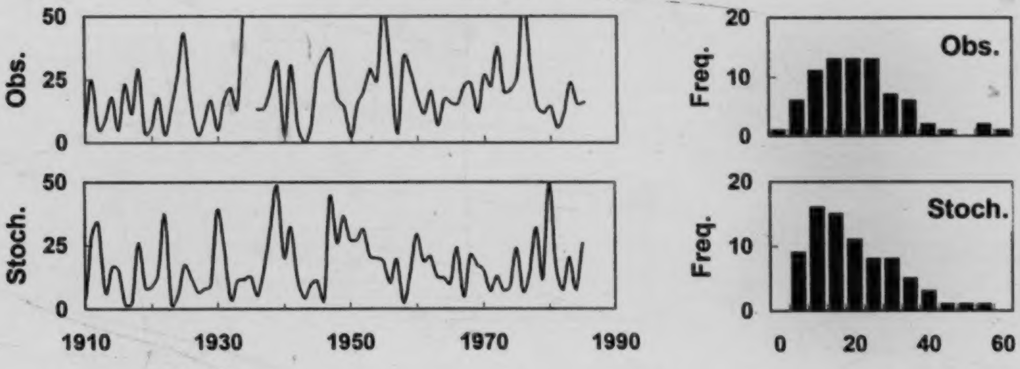


Figure 5-3. Live tree biomass coefficients-of-variation (CVs) from 30 model runs, each using different random seeds. Upper panels (a) and (b) are for BORFOR; lower panels (c) and (d) are for FORSKA2V; left hand panels (a) and (c) are for a typical *P. banksiana* stand and right hand panels (b) and (d) are for a typical *P. tremuloides* stand; open symbols, constant climate; filled symbols, stochastic climate.

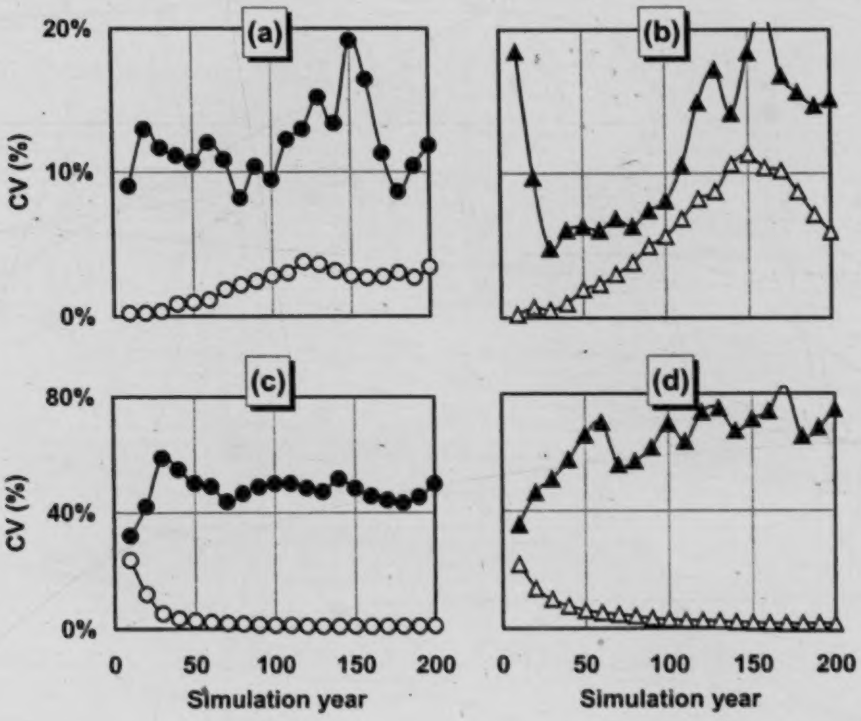


Figure 5-4. Observed versus predicted values for live tree biomass, stem density, snag biomass, forest floor biomass and moss biomass. Observed values are plotted on X-axis and simulated values on Y-axis; filled symbols, BORFOR; open symbols, FORSKA2V; circles, *P. banksiana*; triangles, *P. tremuloides*; sloping line in each panel shows 1:1 correspondence.

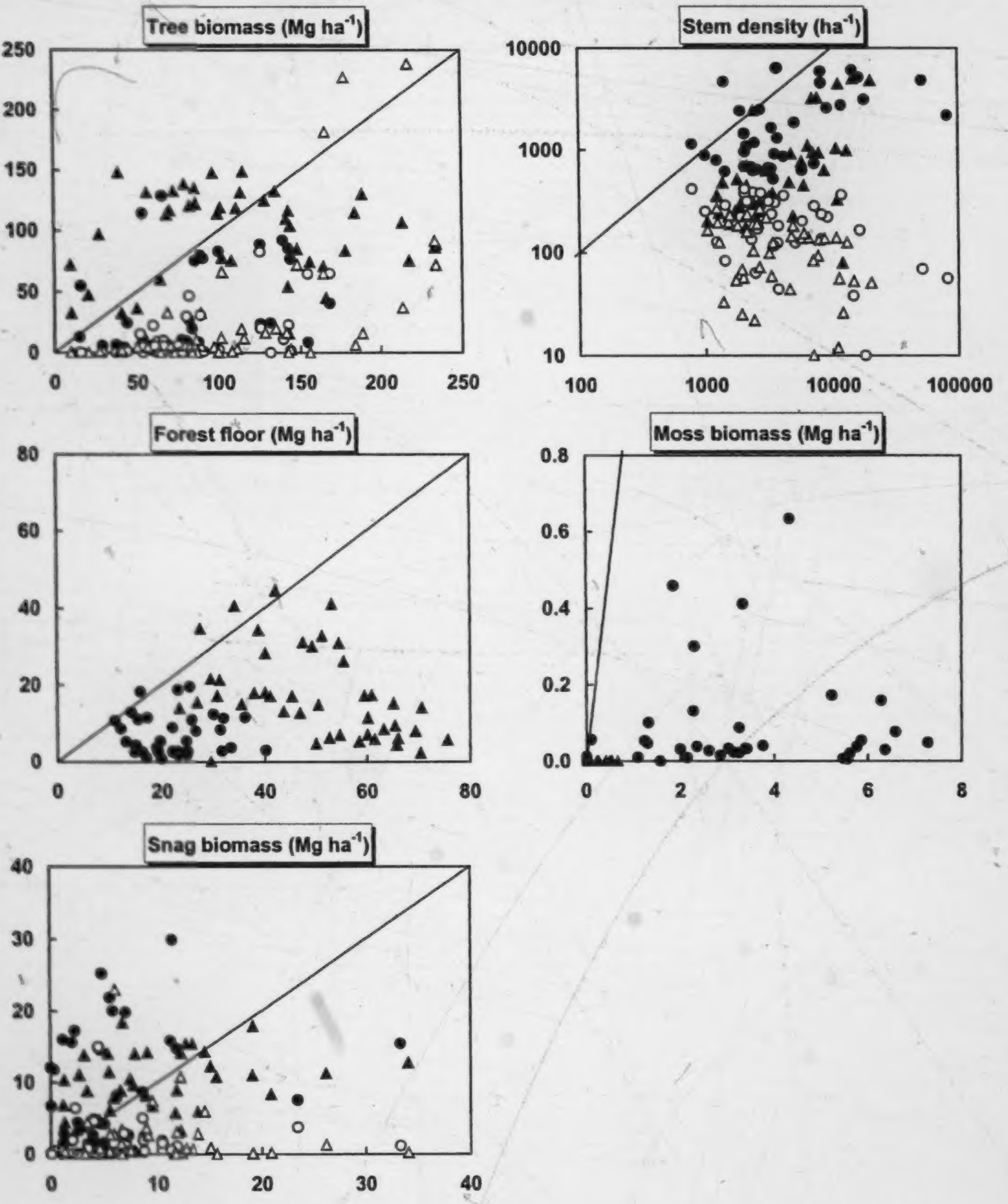
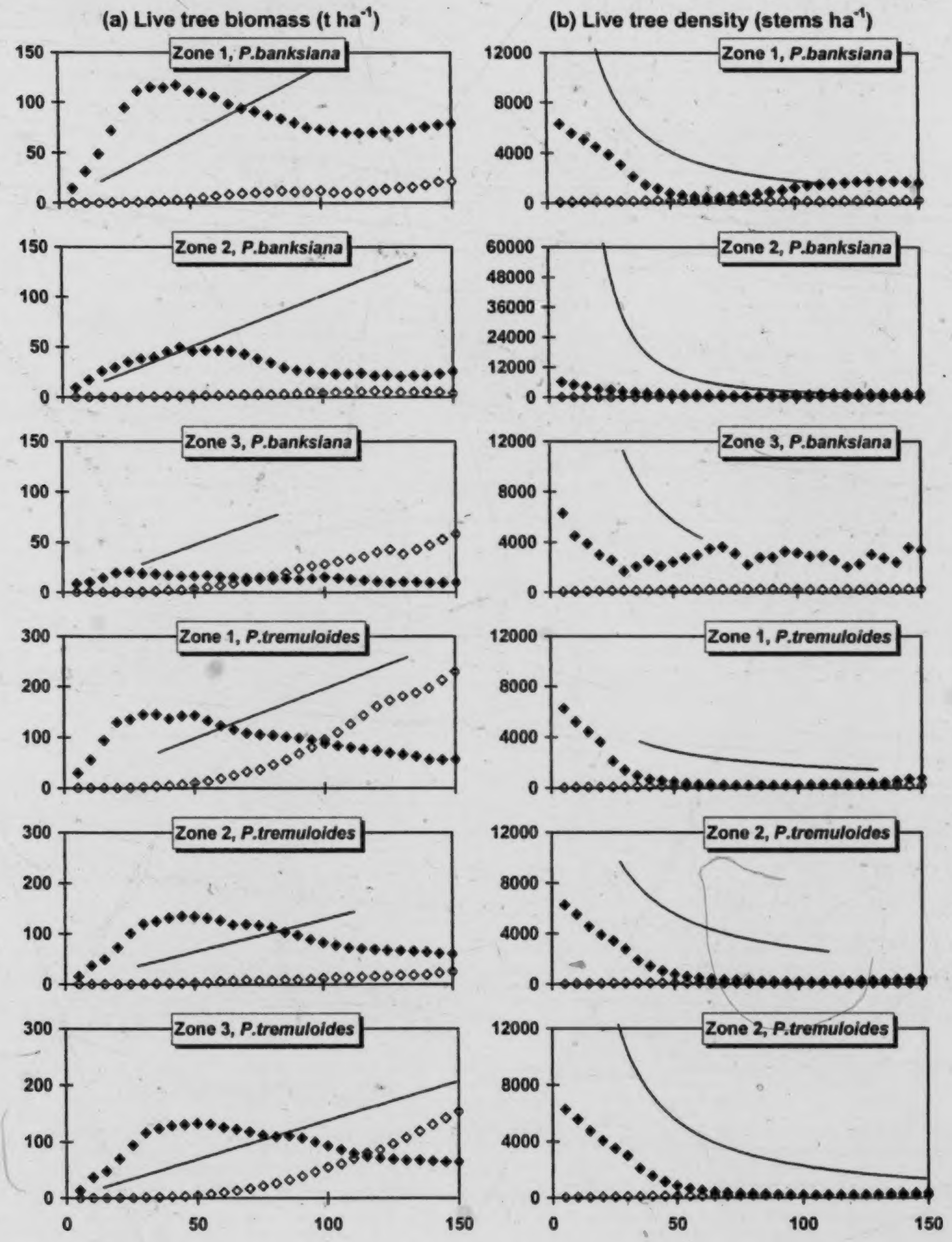


Figure 5-5. Dynamics of (a) live tree biomass and (b) stem density for the six chronosequences simulated in this study showing observed patterns (line), BORFOR simulated patterns (filled symbols) and FORSKA2V simulated patterns (open symbols). R^2 values and models for observed data are given in Table 5-1.



References

Alberta Environmental Protection, 1994. Alberta Vegetation Inventory Standards Manual. Resource Information Development Branch, Land Information Division, Edmonton, Canada. 53 pp.

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G. and Vinson, T.S., 1993. Boreal forests and tundra. Water, Air, Soil Pollut., 70: 39-53.

Beuker, E., Kolstrom, M. and Kellomaki, S., 1996. Changes in wood production of *Picea abies* and *Pinus sylvestris* under a warmer climate: comparison of field measurements and results of a mathematical model. Silva Fennica, 30(2-3): 239-246.

Bonan, G.B., 1989a. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecol. Model., 45: 275-306.

Bonan, G.B., 1989b. Environmental factors and ecological processes controlling vegetation patterns in boreal forests. Landscape Ecology, 3: 111-130.

Bonan, G.B., 1990a. Carbon and nitrogen cycling in North American boreal forests I. Litter quality and soil thermal effects in interior Alaska. Biogeochem., 10: 1-28.

Bonan, G.B., 1990b. Carbon and nitrogen cycling in North American boreal forests II. Biogeographic patterns. Can. J. For. Res., 20: 1077-1088.

Bonan, G.B. and Korzuhin, M.D., 1989. Simulation of moss and tree dynamics in the boreal forests of interior Alaska. Vegetatio, 84: 31-44.

Bonan, G.B. and Shugart, H.H., 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Syst., 20: 1-28.

Bonan, G.B. and Sirois, L., 1992. Air temperature, tree growth, and the northern and southern range limits to *Picea mariana*. J. Veg. Sci., 3: 495-506.

Botkin, D.B., 1993. Forest dynamics: An Ecological Model. Oxford University Press, Oxford. 309 pp.

Botkin, D.B., Janak, J.F. and Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecology, 60: 849-872.

Botkin, D.B. and Nisbet, R.A., 1992. Forest response to climatic change: effects of parameter estimation and choice of weather patterns on the reliability of projections. Clim. Change, 20: 87-111.

Bradley, P., Gaston, G., Kolchugina, T. and Vinson, T.S., 1995. Simulating carbon storage in forests of eastern Russia. Water, Air, Soil Pollut., 82: 299-308.

Brady, N.C., 1990. The Nature and Properties of Soils. Macmillan Publishing Company, New York, N.Y., 621 pp.

Bratley, P., Fox, B.L. and Schrage, L.E., 1983. A Guide to Simulation. Springer-Verlag, New York. 383 pp.

Bugmann, H., 2001a. A comparative analysis of forest dynamics in the Swiss Alps and the Colorado Front Range. For. Ecol. Man., 145(1-2): 43-55.

Bugmann, H., 2001b. A review of forest gap models. Clim. Change, 51(3-3): 259-305.

Bugmann, H. and Cramer, W., 1998. Improving the behaviour of forest gap models along drought gradients. For. Ecol. Man., 103(2-3): 247-263.

Bugmann, H., Wullschleger, S.D., Price, D.T., Ogle, K., Clark, D.F. and Solomon, A.M., 2001. Comparing the performance of forest gap models in North America. Clim. Change, 51(3-4): 349-388.

Bugmann, H.K.M. and Solomon, A.M., 2000. Explaining forest composition and biomass across multiple biogeographical regions. Ecol. Appl., 10(1): 95-114.

Burns, R.M. and Honkala, B.H., 1990. Silvics of North America: Agriculture Handbook 654. USDA Forest Service, Washington, D.C. 2 volumes

Burton, P.J. and Cumming, S.G., 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water, Air, Soil Pollut., 82: 401-414.

Campbell, I.D. and McAndrews, J.H., 1993. Forest disequilibrium caused by rapid Little Ice Age cooling. Nature, 366: 336-339.

Carroll, S.B. and Bliss, L.C., 1982. Jack pine-lichen woodland on sandy soils in northern Saskatchewan and northeastern Alberta. Can. J. Bot., 60: 2270-2282.

Cowling, S.A., Sykes, M.T. and Bradshaw, R.H.W., 2001. Palaeovegetation-model comparisons, climate change and tree succession in Scandinavia over the past 1500 years. J. Ecol., 89(2): 227-236.

Ecoregions Working Group of Canada, 1989. Ecoclimatic Regions of Canada. Ecol. Land Classif. Ser. 23. Environ. Can. Wildl. Serv., Can. Comm. Ecol. Land Classif., Ottawa, Ontario, Canada.

Ehman, J.L., Fan, W.H., Randolph, J.C., Southworth, J. and Welch, N.T., 2002. An integrated GIS and modeling approach for assessing the transient response of forests of the southern Great Lakes region to a doubled CO_2 climate. For. Ecol. Man., 155((1-3) Special Iss.): 237-255.

El-Bayoumi, M.A., Shugart, H.H. and Wein, R.W., 1984. Modelling succession of the eastern Canadian mixedwood forest. Ecol. Model., 21: 175-198.

Environment Canada, 1982. Canadian Climate Normals 1951-1980. Temperature and Precipitation, The North - Y.T. and N.W.T. Atmospheric Environment Service, Environment Canada, Downsview, Ontario, Canada. 56 pp.

Environment Canada, 1983. Canadian Climate Normals 1951-1980. Temperature and Precipitation, Prairie Provinces. Atmospheric Environment Service, Environment Canada, Downsview, Ontario, Canada. 429 pp.

Environment Canada, 1992. The State of Canada's Climate: Temperature change in Canada 1895-1991. State of the Environment Report No. 92-2. Government of Canada, Ottawa, Canada. 36 pp.

Environment Canada, 1994. Canadian Monthly Climate Data and 1961-1990 Normals on CD-ROM, Version 3.0E. CD-ROM Environment Canada, Ottawa, Canada.

Evert, F., 1985. Systems of equations for estimating ovendry mass of 18 Canadian tree species. Inf. Rep. PI-X-59. PNFI, Can. For. Serv., Chalk River, Ontario, Canada.

Fischlin, A., Bugmann, H. and Gyalistras, D., 1995. Sensitivity of a forest ecosystem model to climate parameterization schemes. Environ. Pollut., 87: 267-282.

Gray, S.L., 1995. A descriptive forest inventory of Canada's forest regions. Inf. Rep. PI-X-122. Can. For. Serv., Chalk River, Ontario, Canada.

Grigal, D.F., Brovold, S.L., Nord, W.S. and Ohmann, L.F., 1989. Bulk density of surface soils and peat in the North Central United States. Can. J. Soil Sci., 69: 895-900.

He, H.S., Mladenoff, D.J. and Crow, T.R., 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecol. Model., 114(2-3): 213-233.

He, H.S., Mladenoff, D.J. and Gustafson, E.J., 2002. Study of landscape change under forest harvesting and climate warming-induced fire disturbance. For. Ecol. Man., 155(1-3 Special Iss.): 257-270.

Heathcott, M.J. and Cornelsen, S.C., 1994. Options for fire management in Wood Buffalo National Park. In: Duncan, T.A., Forster, W.A.D. and Lanoville., R.A., (Editors). Managing Fire Dependent Ecosystems: Options and Technologies. Proceedings from 1992 Interior West Fire Council Annual Meeting October 27-29, 1992, Yellowknife, NWT. Govt. Northwest Territories, pp. 75-85.

Hogg, E.H., 1999. Simulation of interannual responses of trembling aspen stands to climatic variation and insect defoliation in western Canada. Ecol. Model., 114: 175-193.

Hogg, E.H. and Schwarz, A.G., 1997. Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. J. Biogeogr., 24: 527-534.

Hogg, T.H., 1994. Climate and the southern limit of the western Canadian boreal forest. Can. J. For. Res., 24: 1835-1845.

Johnson, E.A., 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. Ecology, 62: 200-215.

Johnson, E.A., 1992. Fire and Vegetation Dynamics. Cambridge University Press, Cambridge, UK. 129 pp.

Kangas, A.D., 1998. Uncertainty in growth and yield projections due to annual variation of diameter growth. For. Ecol. Man., 108(3): 223-230.

Karjalainen, T., 1996a. The carbon sequestration potential of unmanaged forest stands in Finland under changing climatic conditions. Biomass Bioenergy, 10(5-6): 313-329.

Karjalainen, T., 1996b. Model computations on sequestration of carbon in managed forests and wood products under changing climatic conditions in Finland. J. Env. Manage., 47(4): 311-328.

Kasischke, E.S., Christensen Jr., N.L. and Stocks, B.J., 1995. Fire, global warming, and the carbon balance of boreal forests. Ecol. Appl., 5: 437-451.

Kattenberg, A., Giorgi, G., Grassl, H., Meehl, G.A., Mitchell, J.F.B., Stougger, R.J., Tokioka, T., Weaver, A.J. and Wigley, T.M.L., 1996. Climate models - projections of future climate. In: Houghton, J.T., Meira Filho, J.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K., (Editors). Climate Change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, UK, pp. 283-357.

Kauppi, P.E., Posch, M., Hanninen, P., Henttonen, H.M., Ihalainen, A., Lappalainen, E., Starr, M. and Tamminen, P., 1997. Carbon reservoirs in peatlands and forests in the boreal regions of Finland. Silva Fennica, 31(1): 13-25.

Kellomäki, S., 1995. Computations on the influence of changing climate on the soil moisture and productivity in Scots pine stands in southern and northern Finland. Clim. Change, 29: 35-51.

Kellomäki, S., Hänninen, H. and Kolström, M., 1995. Computations on frost damage to Scots pine under climatic warming in boreal conditions. Ecol. Appl., 5: 42-52.

Kellomäki, S. and Kolström, M., 1992. Simulation of tree species composition and organic matter accumulation in Finnish boreal forests under changing climatic conditions. Vegetatio, 102(1): 47-68.

Kellomäki, S. and Kolström, M., 1993. Computations on the yield of timber by Scots pine when subjected to varying levels of thinning under changing climatic in southern Finland. For. Ecol. Man., 59: 237-255.

Kellomäki, S. and Kolström, M., 1994. The influence of climate change on the productivity of Scots pine, Norway spruce, Pendula birch and Pubescent birch in southern and northern Finland. For. Ecol. Man., 65: 201-217.

Kellomäki, S. and Väisänen, H., 1995. Model computations on the impact of changing climate on natural regeneration of Scots pine in Finland. Can. J. For. Res., 25: 929-942.

Larsen, C.P.S., 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeogr., 24: 663-673.

Larsen, C.P.S. and MacDonald, G.M., 1995. Relations between tree-ring widths, climate, and annual area burned in the boreal forest of Alberta. Can. J. For. Res., 25: 1746-1755.

Lee, P., 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Man., 105: 263-272.

Lexer, M.J. and Honninger, K., 2001. A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. For. Ecol. Man., 144(1-3): 43-65.

Lindner, M., Lasch, P. and Cramer, W., 1996. Application of a forest succession model to a continentality gradient through Central Europe. Clim. Change, 34(2): 191-199.

Lindner, M., Sievanen, R. and Pretzsch, H., 1997. Improving the simulation of stand structure in a forest gap model. For. Ecol. Man., 95: 183-195.

Liski, J. and Westman, C.J., 1997. Carbon storage in forest soil of Finland: 1. Effect of thermocline. Biogeochem., 36: 239-260.

Loehle, C. and LeBlanc, D., 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol. Model., 90: 1-31.

Makipaa, R., Karjalainen, T., Pussinen, A. and Kukkola, M., 1998. Effects of nitrogen fertilization on carbon accumulation in boreal forests: Model computations compared with the results of long-term fertilization experiments. Chemosphere, 36(4-5): 1155-1160.

Murphy, P.J., 1985. Methods for evaluating the effects of forest fire management in Alberta. Ph.D. thesis, Faculty of Forestry, University of British Columbia, Vancouver, B.C. 167 pp.

Nalder, I.A. and Merriam, H.G., 1995. Simulating carbon dynamics of the boreal forest in Pukaskwa National Park. Water, Air, Soil Pollut., 82: 283-298.

Nalder, I.A. and Wein, R.W., 1998a. A new forest floor corer for rapid sampling, minimal disturbance and adequate precision. Silva Fennica, 32(4): 373-382.

Nalder, I.A. and Wein, R.W., 1998b. Spatial interpolation of climatic Normals: test of a new method in the Canadian boreal forest. Agric. For. Meteorol., 92(4): 211-225.

Nalder, I.A. and Wein, R.W., 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochem. Cycles, 13(4): 951-968.

Nisbet, R.A. and Botkin, D.B., 1993. Vegetation feedbacks and the prediction of future fluxes of the global carbon cycle. In: Vinson, T.S. and Kolchugina, T.P. (Editors). Biospheric Responses and Feedbacks to Global Climate Change: Proceedings of the International Workshop on carbon cycling in the Boreal Forest and Sub-Arctic Ecosystems, U.S. Environmental Protection Agency, Corvallis, Oregon, pp. 209-214.

NOAA/NGDC, 1992. Global Ecosystems Database Version 1.0 Disc A. NOAA National Geophysical Center, Boulder, Colorado.

Overpeck, J.T., Rind, D. and Goldberg, R., 1990. Climate-induced changes in forest disturbance and vegetation. Nature, 343: 51-53.

Pastor, J. and Post, W.M., 1988. Response of northern forests to CO_2-induced climatic change. Nature, 334: 55-58.

Peterson, E.B. and Peterson, N.M., 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. Spec. Rep. 1. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta.

Peterson, T.C. and Vose, R.S., 1997. An overview of the Global Historical Climatology Network temperature data base. Bull. Am. Meteorol. Soc., 78: 2837-2849.

Post, W.M. and Pastor, J., 1996. Linkages - an individual-based forest ecosystem model. Clim. Change, 34(2): 253-261.

Post, W.M., Pastor, J., King, A.W. and Emanuel, W.R., 1992. Aspects of the interactions between vegetation and soil under global change. Water, Air, Soil Pollut., 64: 345-363.

Prentice, I.C., Sykes, M.T. and Cramer, W., 1991. The possible dynamic response of northern forests to global warming. Global Ecology and Biogeography Letters, 1: 129-135.

Prentice, I.C., Sykes, M.T. and Cramer, W., 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecol. Model., 65: 51-70.

Price, D.T. and Apps, M.J., 1993. Use of a forest ecosystem level model to investigate responses of boreal landscape productivity to climate. In: Proceedings of Forestry Canada Modelling Working Group Workshop, February 1993, Victoria, B.C., pp. 10-17.

Price, D.T. and Apps, M.J., 1996. Boreal forest responses to climate-change scenarios along an ecoclimatic transect in Central Canada. Clim. Change, 34(2): 179-190.

Price, D.T., Apps, M.J., Kurz, W.A., Prentice, I.C. and Sykes, M.T., 1993. Simulating the carbon budget of the Canadian boreal forest using an integrated suite of process-based models. In: Ung, C.-H. (Editor). Proceedings of the International Workshop: Forest Growth Models and their Uses, November 1993, Quebec City, Quebec, pp. 251-264.

Price, D.T., Halliwell, D.H., Apps, M.J. and Peng, C.H., 1999a. Adapting a patch model to simulate the sensitivity of Central-Canadian boreal ecosystems to climate variability. J. Biogeogr., 26: 1101-1113.

Price, D.T., Peng, C.H., Apps, M.J. and Halliwell, D.H., 1999b. Simulating effects of climate change on boreal ecosystem carbon pools in central Canada. J. Biogeogr., 26: 1101-1113.

Pussinen, A., Karjalainen, T. and Kellomaki, S., 1997. Contribution of the forest sector in carbon sequestration under changing climate conditions in Finland. In: Sustainable Development of Boreal Forests: Proceedings of the 7th Annual Conference of the IBFRA, August 19-23, 1996, St. Petersburg, Moscow, Russia, International Boreal Forest Research Association/Forest Service of Russia, pp. 76-85.

Richardson, C.W., 1981. Stochastic simulation of daily precipitation, temperature, and solar radiation. Wat. Resour. Res., 17(1): 182-190.

Schenk, H.J., 1996. Modelling the effects of temperature on growth and persistence of tree species: a critical review of tree population models. Ecol. Model., 92: 1-32.

Schimel, D., Alves, D., Enting, I., Heimann, M., Joos, F., Raynaud, D., Wigley, T., Prather, M., Derwent, R., Ehhalt, D., Fraser, P., Sanhueza, E., Shou, X., Jonas, P., Charlson, R., Rodhe, H., Sadasivan, S., Shine, K.P., Fouquart, Y., Ramaswamy, V., Solomon, S., Srinivasan, J., Albritton, D., Derwent, R., Isaksen, I., Lal, M. and Wuebbles, D., 1996. Radiative forcing of climate change. In: Houghton, J.T., Meira Filho, J.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K., (Editors). Climate Change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, UK, pp. 65-131.

Sellers, P.J., Hall, F.G., Kelly, R.D., Black, A., Baldocchi, D., Berry, J., Ryan, M., Ranson, K.J., Crill, P.M., Lettenmaier, D.P., Margolis, H., Cihlar, J., Newcomer, J., Fitzjarrald, D., Jarvis, P.G., Gower, S.T., Halliwell, D., Williams, D., Goodison, B., Wickland, D.E. and Guertin, F.E., 1997. BOREAS in 1997: Experiment overview, scientific results, and future directions. J. Geophy. Res., 102(D24): 28731-28769.

Shugart, H.H., 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York. 278 pp.

Siltanen, R.M., Apps, M.J., Zoltai, S.C., Mair, R.M. and Strong, W.L., 1997. A soil profile and organic carbon data base for Canadian forest and tundra mineral soils. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, Canada. 50 pp.

Sirois, L., Bonan, G.B. and Shugart, H.H., 1994. Development of a simulation model of the forest-tundra transition zone of northeastern Canada. Can. J. For. Res., 24: 697-706.

Solomon, A.M., 1985. Computer-aided reconstruction of late-Quaternary landscape dynamics. Ann. Rev. Ecol. Syst., 16: 63-84.

Solomon, A.M., 1986. Transient response of forests to CO2-induced climate change: simulation modeling experiments in eastern North America. Oecologia, 68: 567-579.

Solomon, A.M., Tharp, M.L., West, D.C., Taylor, G.E., Webb, J.M. and Trimble, J.C., 1984. Response of unmanaged forests to CO_2-induced climate change: available information, initial tests, and data requirements. Report TR009. Oak Ridge National Lab., Oakridge, TN.

Sykes, M., 2001. Modelling the potential distribution and community dynamics of lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) in Scandinavia. For. Ecol. Man., 141(1-2): 69-84.

Sykes, M.T. and Prentice, I.C., 1995. Boreal forest futures: modelling the controls on tree species range limits and transient responses to climate change. Water, Air, Soil Pollut., 82: 401-414.

Sykes, M.T. and Prentice, I.C., 1996a. Carbon storage and climate change in Swedish forests: a comparison of static and dynamic modelling approaches. In: Apps, M.J. and Price, D.T., (Editors). The Role of Forest Ecosystems, Forest Management and the Global Carbon Cycle. Proceedings of the NATO Advanced Research Workshop held at Banff, Canada, September 12-16, 1994. Springer, Berlin, pp. 69-78.

Sykes, M.T. and Prentice, I.C., 1996b. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. Clim. Change, 34(2): 161-177.

Van Wagner, C.E., 1978. Age-class distribution and the forest fire cycle. Can. J. For. Res., 8: 220-227.

Viereck, L.A., 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. In: Wein, R.W. and McLean, D.A., (Editors). The Role of Fire in Northern Circumpolar Ecosystems. John Wiley & Sons, Chichester, UK, pp. 201-220.

Weir, J.M.H. and Johnson, E.A., 1998. Effects of escaped settlement fires and logging on forest composition in the mixedwood boreal forest. Can. J. For. Res., 28: 459-467.

Westoby, M., 1984. The self-thinning rule. Adv. Ecol. Res., 14: 167-225.

Woodwell, G.M., Mackenzie, F.T., Houghton, R.A., Apps, M., Gorham, E. and Davidson, E., 1998. Biotic feedbacks in the warming of the earth. Clim. Change, 40(3-4): 495-518.

Yarie, J., Pulliam, W., Van Cleve, K. and Schlenter, R., 1995. Carbon and nutrient availability effect on plant nutrient supply for upland forest sites in interior Alaska. N. Z. J. For. Res., 24(2/3): 234-252.

6. A model of post-fire forest floor dynamics in the continental boreal forest of western Canada

Introduction

Northern ecosystems are increasingly recognized as playing an important role in climate change (Woodwell et al., 1998; Chapin III et al., 2000). Boreal forests may form an important biotic feedback because they store large amounts of carbon (Apps et al., 1993), which can be sensitive to climate, particularly temperature (Kauppi et al., 1997; Liski and Westman, 1997) and temperature increases in boreal regions are likely to be relatively large, according to projections of general circulation models (GCMs) (Kattenberg et al., 1996). The potential for feedbacks is clear; however, their magnitude and sign remain uncertain.

In upland forests, the forest floor is a substantial pool of carbon which is likely to be sensitive to climate change (Nalder and Wein, 1999). It also acts as an important control on many key processes such as nutrient cycling (Chapter 1). These processes may be more important than aboveground processes in determining long-term productivity responses to increasing temperature and CO_2 (Medlyn et al., 2000). Consequently, it is important to be able to predict how the forest floor changes throughout the life of a stand to assess the impacts of climate change. These dynamics, however, have been little studied, particularly over the long-term (decades to centuries).

Because of the long timescales involved with climate change, experimental data are difficult to acquire and assessments of impacts often rely on computer models. No suitable models exist, however, for the western Canadian boreal forest. Patch models, also termed gap dynamics models, have been frequently used for climate change studies in boreal forests but can give unreliable predictions outside their region of parameterization (Chapter 5 and Bugmann et al., 2001). Also many of these models do not explicitly represent the forest floor (e.g., Burton and Cumming, 1995; Price et al., 1999). Of those that do, decay is generally represented as a first-order process based on short-term decay studies (e.g., Bonan, 1990b; Post and Pastor, 1996; Makipaa et al., 1999), but there is mounting evidence that this is not appropriate for the longer term (e.g., Parton et al., 1987; Parton et al., 1988; Berg and Ekbohm, 1991; Trumbore, 1993; Townsend et al., 1995; Liski et al., 1998; Giardina and Ryan, 2000).

The CENTURY model (Parton et al., 1987; Parton et al., 1993) provides an alternative model of soil organic matter decomposition based on concepts from agricultural systems. It is well validated and has proved robust in predicting mineral soil C across a range of ecosystems (Parton et al., 1988; Parton et al., 1989; Ojima et al., 1993; Parton et al., 1993; Trumbore, 1993; Parton and Rasmussen, 1994; Vitousek et al., 1994; Yarie et al., 1995; Smith et al., 1997). It has successfully been applied to predict mineral soil C at several sites in the continental boreal forest of western Canada (Peng et al., 1998). However, CENTURY has a number of limitations. First, it does not explicitly represent the forest floor as a separate soil layer, a limitation previously noted for forest applications (Kelly et al., 1997). Second, the tree growth routines and parameters are not species-specific: reparameterization, if feasible, is beyond the scope of this study. Third, CENTURY does not represent other vegetation such as shrubs and moss which can be important components (Nalder and Wein, 1999). Fourth, the abiotic multipliers were developed for U.S.

grasslands and there are serious questions, addressed further in the Methods section, about their applicability to boreal forests.

Here a new model is developed to simulate forest floor carbon dynamics. This is a carbon input-output model based on the CENTURY decay routines but with new input and abiotic multiplier routines to address the above limitations. The model is part of a wider study into forest floor dynamics. The study focuses on upland forests in the Boreal West Ecoclimatic Province of Canada (Ecoregions Working Group of Canada, 1989; Siltanen et al., 1997). This region will be referred to as the western boreal. It is formed by a 1000 km wide arc of continental boreal forest that stretches from the Ontario/Manitoba border west and north to the base of the western mountain chain in Alberta and the Northwest Territories. It is of particular interest because it appears particularly sensitive to climate change: it has undergone 1.3-1.7 °C warming over the last century (Environment Canada, 1992) and GCM projections indicate it will undergo greenhouse warming much greater than the global average in the future (Kattenberg et al., 1996). At the same time, research from other boreal regions can provide only limited guidance because conditions in the western boreal are unique. It currently receives lower precipitation than Canada's eastern boreal while radiation regimes are quite different from interior Alaska to the west. Compared with northern Scandinavia, the climate is drier, colder and more continental, and the suite of native tree species is different. Similar climatic conditions do exist in continental Siberia, but winters there tend to be colder and the different history of deglaciation has led to larch and pine being dominant over much of the landscape.

The objective of this study is to develop a simple but realistic model of forest floor dynamics to interpret the results of previous field studies, particularly to explain the effect of age, species and climate on forest floor carbon, and to identify major controlling variables on forest floor dynamics and critical areas for further research. The study is limited to upland stands dominated by *Populus tremuloides* Michx. (trembling aspen) and *Pinus banksiana* Lamb. (jack pine). These species together account for 50% of timber volume in the western boreal and dominate upland areas.

Methods

General methodology

The model simulates carbon flows through the forest floor and mineral soil (Figure 6-1). The empirically derived inputs are the various forms of litter and outputs are the losses due to decay or removal by fire. Nitrogen cycling is also simulated. The model includes three submodels. Vegetation stocks and litterfall are calculated in the GROWTH submodel. Vegetation stocks are related to stand age and other significant variables by regressions of field data from a previous study (Nalder and Wein, 1999) which examined six chronosequences, one for each of two tree species in three climatic zones. Carbon stocks are defined for each of 18 components, such as tree foliage or snags. For each component, annual litter input to the forest floor is calculated from stocks using various literature relationships. Litter is consolidated and decomposed in the DECAY submodel using the algorithms developed for the CENTURY model (Parton et al., 1987; Parton et al., 1993). The decay rates in these algorithms are modified by multipliers for suboptimal temperature and moisture conditions. These multipliers are calculated in the CLIMATE submodel based on monthly climatic Normals. After validation against independent data and field data from the chronosequence studies, the model is used to simulate forest floor carbon dynamics for each of the species and climatic zones. It is then used to explore reasons for observed dynamics, to explain any discrepancies and to identify critical but poorly understood areas which require further research.

Field data

Climatic zones

Upland forest stands were sampled in three distinct climatic zones (Figure 6-2). These zones were chosen to provide contrasting extremes of temperature and precipitation within the western boreal. Stands were selected within or close to the Southern Study Area (SSA) of the BOReal Ecosystem-Atmosphere Study (BOREAS) (Sellers et al., 1997) near Prince Albert, Saskatchewan (zone 1), in Wood Buffalo National Park near Fort Smith (zone 2), and within or close to the BOREAS Northern Study Area (NSA) centred on Thompson, Manitoba (zone 3). These zones represent warm-dry, cold-dry and cold-moist conditions respectively (Table 6-1).

Chronosequences

Within each climatic zone stands of various ages (time since stand-replacing fire) that were dominated by *P. banksiana* or *P. tremuloides* were sampled to provide a chronosequence of at least 10 stands for each species and zone. For each stand, latitude, longitude, elevation, slope, aspect, stand age, and amount of trees, shrubs and ground vegetation were determined. Biomass of each component of vegetation was estimated from allometric equations (see next paragraph). Using a specially designed corer (Nalder and Wein, 1998a), ten soil cores were taken and used to measure forest floor organic matter using loss-on-ignition (LOI), forest floor depth and bulk density, and moss-plus-lichen biomass. For the underlying mineral soil, depth to impermeable layer was measured. For the upper 20 cm layer of mineral soil, texture was estimated in the field, organic matter content was determined by loss-on-ignition and bulk density calculated using the relationships of Grigal (1989). Moisture contents at saturation, field capacity and wilting point were determined using a pressure plate apparatus. These stand sampling and measurements are described in more detail in Nalder and Wein (1999); the main characteristics of each chronosequence are reproduced in Table 6-1.

Vegetation stocks

In each stand, the biomass of each live tree stem (stemwood plus stem bark) and crown was calculated from the allometric relationships of Evert (1985). Crown biomass was apportioned to branches and foliage using the following relationships derived from allometric data in Alban (1982) and Johnstone and Peterson (1980):

Foliage biomass (*P. banksiana*) = 0.25 * Crown biomass ....(1)

Foliage biomass (*P. tremuloides*) = (0.1914 - dbh(cm) / 350) * Crown biomass ....(2)

For dead trees, biomass was estimated as for live trees, except that crown biomass was assumed to be zero. A small number of dead trees had broken off below the crown, generally 2-4 m above ground, and biomass of these was approximated assuming a cylinder of radius dbh/2 with density of 0.5 Mg m^{-3}. For each shrub, woody biomass and foliage biomass were calculated from basal diameter using the allometric equations of Roussopoulos and Loomis (1979). Ground vegetation (dwarf shrubs, forbs, legumes, grasses) was also tallied, but its biomass was small relative to shrubs and trees (Nalder and Wein, 1999); consequently, it was judged unlikely to be a significant contributor to litter and is not considered further.

For each vegetation component, stand means were calculated as biomass per unit area then converted to C density assuming the commonly used value of 50% C content (Grigal and Ohmann, 1992; Kurz et al., 1992; Kolchugina and Vinson, 1993; Kauppi et al., 1995; Liski and Westman, 1995; Karjalainen, 1996). Counts were also made of the number of tree stems in each plot, and the stand-level mean stem density (stems/ha) was calculated. Canopy height for each stand was estimated from individual tree height data by taking the mean height of the 10 tallest trees (or the tallest quartile if fewer than 40 trees were tallied) after removing obvious outliers.

Moss-plus-lichen C density for each stand was calculated from the mean oven-dry weight of live moss and lichen in the 10 soil cores divided by the cross sectional area, and converting to organic C assuming a conversion factor of 0.5 as for other vegetation.

For each of the six live vegetation components, general linear regressions (GLM) (SPSS Inc., 1996) were carried out to relate stand-level C density to age as well as other significant variables such as species and mean annual temperature. GLM's were also carried out for stem density and canopy height. Models were chosen to provide the best fit with all terms significant. All equations, except stem density, were forced through the origin on the assumption that chronosequences began with an intense stand-replacing fire that removed all live biomass: this was a condition for selection of stands (Nalder and Wein, 1999). For stem C density, logistic forms were tested because they are often appropriate for stem volume, but they gave poor fits and the data showed no evidence of upper asymptotes. The lack of an upper asymptote is probably due to the slow C accumulation rates in the western boreal, e.g., pine and hardwood Yield Curves for Alberta show no evidence of an upper asymptote in volume per hectare for at least 180 years (Alberta Forest Service, 1985). Stem density was a log-log function which closely approximated the self-thinning rule (Westoby, 1984); the upper bound was truncated at 10^5 stems ha^{-1} based on literature data for the study region (Carroll and Bliss, 1982; Peterson and Peterson, 1992). The regression models are summarized in Table 6-2.

Climate data

For each stand, climatic variables were estimated by spatially interpolating from surrounding climate stations using the "Gradient-plus-Inverse Distance Squared" (GIDS) technique (Nalder and Wein, 1998b) and 1951-1980 monthly Normals (Environment Canada, 1982; Environment Canada, 1983). Monthly climatic Normals were mean and standard deviation of temperature and precipitation, and mean maximum and mean minimum temperature. Additinally, monthly mean solar radiation was taken from McKay and Morris (1985), digitized to a grid, then interpolated to stand locations using the GIDS technique.

Model outline

The following section describes the computer simulation model upon which this study is based. For convenience, it will be referred to as CIOM (Carbon Input-output Model). Apart from housekeeping routines, CIOM consists of three submodels: GROWTH, CLIMATE and DECAY, which will be described in turn.

GROWTH submodel

Vegetation growth

Carbon density of tree foliage, branches and stems, shrub foliage and wood, and moss-plus-lichen was calculated as a function of stand age from the regression models of Table 6-2 (see Figure 6-3). No suitable data exist to allow roots and stump biomass to be calculated in the same manner as aboveground components of trees and shrubs. However, a review of published stand-level stump and root biomass data (Strong and La Roi, 1983a; Ruark and Bockheim, 1987; Peterson and Peterson, 1992) revealed distinct patterns relating aboveground and below-ground biomass per hectare (Figure 6-4). These relationships, which applied to both species, were used to calculate stump, coarse root and fine root C density for each stand as a function of stem C density. Here "roots" refers to live roots of all species, including shrubs, with a threshold of 5 mm separating coarse and fine roots.

Stem density and canopy height were calculated from the regression models of Table 6-2. Mean dbh of trees in a stand was estimated from height-dbh relationships for *P. banksiana* and *P. tremuloides* in Alberta (Function 4 of Huang et al., 1992). Distribution of fine root biomass by depth was estimated based on the observation that fine root and total root biomass decreases exponentially with depth through forest floor and mineral soil (e.g., Persson, 1983, Figure 1; Tryon and Chapin III, 1983, Figure 6; Ruark and Bockheim, 1987, Table 1; Jackson et al., 1996, Figure 1; Finer et al., 1997, Figure 1; Widen and Majdi, 2001, Table 2). Thus fine root biomass, B_{fr}, in any soil layer below the top of the forest floor can be given by:

$$B_{fr} = \frac{A}{m}\left(e^{z_1 m} - e^{z_2 m}\right) \quad \text{......} (4)$$

where A and m are coefficients representing the intercept and slope, respectively, on a logarithmic plot, and z_1 and z_2 are the lower and upper depths (cm). The values of m are -0.04295 and -0.04905 for *P. banksiana* and *P. tremuloides*, respectively, based on root density data for typical soils in Central Alberta (Strong and La Roi, 1983b). For any root biomass, the coefficient A is calculated from the above equation assuming a maximum rooting depth of 100 cm. It is assumed that coarse roots have the same distribution as fine roots and that stump biomass is distributed evenly between the forest floor and the upper layer of mineral soil.

Litter from live vegetation

During the life of a stand, annual litter is calculated for each vegetation component. Foliage litter is defined by foliage retention time. For deciduous species (*P. tremuloides* and shrubs) it is set to 1 year; for *P. banksiana*, it is set to 4 years based on leaf age data from the BOREAS old and young jack pine sites (Gower et al., 1997). Fine root litter is defined by fine root retention time. Reported values of fine root turnover times for *P. banksiana* and *P. tremuloides* vary by an order of magnitude (Kurz et al., 1996; Ruess et al., 1996; Steele et al., 1997); in the absence of good data, fine root retention time is taken to be 2 years. Annual moss-plus-lichen litter is calculated as 20.4% of C stocks (Bonan, 1990a). Live tree stems, stumps and coarse roots, as well as shrub wood, do not contribute any litter, i.e., they only become litter when they die. Tree branch litter is estimated by assuming that it is derived solely from self pruning, that branch biomass is spread uniformly throughout the crown and that the crown base is a fixed percentage of tree height. With these assumptions, tree branch litter, $L_{b(t)}$, for year t is given by:

$$L_{b(t)} = B_{b(t-1)}\left(\frac{H_{(t)}}{H_{(t-1)}}-1\right)\bigg/\left(\frac{1}{C}-1\right) \quad\text{.......} (5)$$

where H is tree height (m), C is crown base as a fraction of tree height, and B_b is branch biomass. All trees heights are assumed to be equal to canopy height, calculated from the regression model of Table 6-2. The value of C is 0.61 for *P. tremuloides* (Peterson and Peterson, 1992, Table 4) and 0.50 for *P. banksiana* (pers. observation).

Litter from tree mortality

Litter from dead trees may also form a significant input to the forest floor. Tree mortality may occur from self thinning or fire (see following sub-sections). Other disturbances are important, but are beyond the scope of this study. In either case, trees that die contribute foliage and roots to the litter pool in the year of death. Stem, branch and stump biomass become litter inputs to the soil after a substantial delay because dead trees can remain standing as snags for many years, and even after falling, can remain propped above the forest floor for several more years as logs (coarse woody debris). Few data exist for these dynamics. The model represents snags by a Weibull function with a shape factor of 1.5 and with average time to fall after a stand-replacing fire of 10 and 5 years for *P. banksiana* and *P. tremuloides*, respectively. Trees that die from self thinning as opposed to fire can be expected to remain standing longer because they are sheltered from wind by the surrounding live trees; in this case, the average time to fall is assumed to be twice that of fire-killed trees. These assumptions apply to trees of dbh greater than 20 cm; smaller trees can be expected to fall in a shorter time, therefore average time to fall is assumed to be linearly related to dbh for stands where the mean dbh is less than 20 cm. These assumptions give patterns that are consistent with an ongoing study of post-fire breakdown in progress in Wood Buffalo National Park (R. W. Wein, pers. comm.) and with data for breakdown in *P. tremuloides* stands in Alberta (Lee, 1998). It is further assumed that fallen snags remain on or above the forest floor for twice the period of time that they were snags before being incorporated into the forest floor. During this period, dead tree biomass (comprising stems, branches and stumps) decays at 3.3 and 4.5% per year for *P. banksiana* and *P. tremuloides*, respectively, based on long-term decomposition studies of Scots pine and birch in North west Russia (Krankina and Harmon, 1995). At the end of this period, stem and branch C is added to the forest floor litter input for that year, and stump C is divided evenly between the forest floor and mineral soil litter inputs. The model also tracks rotten log content of the forest floor for comparison with field data (Nalder and Wein, 1999), where rotten logs are defined as stem and stump litter derived from trees that were greater than 10 cm dbh.

Self thinning of trees

Tree mortality from self thinning in any year is the difference in stem density from the previous year to the current year, where stem density is calculated from the regression model of Table 6-2. Such trees are usually strongly suppressed before they die, therefore it is assumed that the individual biomass of each component is 50% of the average for each tree in the stand based on field observations.

Fire effects

All stands are assumed to regenerate from an intense stand-replacing fire for comparability with field data (Nalder and Wein, 1999). Fire removes all fine fuel, taken to be all shrub, moss, lichen and tree foliage biomass, as well as snag and log biomass. Fire also removes

50% of tree stem and stump biomass, and 60% of tree branch biomass (MacLean and Wein, 1980, Table 1), with the remainder becoming snag stem, stump and branch biomass, respectively. For *P. tremuloides*, 75% of the forest floor is removed (Quintilio et al., 1991, Table 3); for *P. banksiana*, 90% of the forest floor is removed, which accords with field observations that intense fires consume nearly all of the forest floor in these stands. Litter, which is separately tracked in the DECAY submodel (structural and metabolic pools), is removed first and the remainder of the forest floor (active, slow and passive pools) is removed in proportion to achieve the above percentages. Forest floor depth is calculated from:

$$D = a \times \ln(FFC + 1) + b \quad \text{.....} (6)$$

where D is forest floor depth (cm), a is a parameter equal to 6.821, b is a parameter equal to -1.765 cm for *P. banksiana* and -0.561 cm for *P. tremuloides* and FFC is forest floor C density (kgC m^{-2}). This equation and parameters were derived from a regression model of observed depths and ln (FFC+1) ($R^2 = 0.98$). There were no data for FFC less than 0.7 kgC m^{-2} therefore a linear relationship with depth is assumed below this point. Pre- and post-fire forest floor depths are used to calculate root biomass removed by fire based on the root distribution (Equation 4). For *P. banksiana*, the remaining root biomass becomes root litter. For *P. tremuloides*, where some roots form the base for sucker regeneration, root litter is taken as the difference between root biomass for the year of the fire and the year after fire.

Seasonal litter distribution

The DECAY submodel takes litter input in monthly timesteps. For input to the DECAY submodel, annual litter is distributed over 12 months as per Table. 6-3 based on published litterfall data for surface litter (Cragg et al., 1977; Weber, 1987), and typical patterns of NPP for below-ground litter assuming root turnover is proportional to NPP.

Nitrogen and Lignin

Nitrogen uptake is equal to the C uptake of each component divided by the C:N ratio of that component. Litterfall nitrogen is calculated similarly. In addition, N released from the decay of dead trees in any year is added to the forest floor litter N input for that year. Lignin content of litter is calculated from C content and lignin fraction. C:N ratios and lignin fractions of each component are listed in Table 6-4.

CLIMATE submodel

Climatic variables

The model uses a variable climate following Bonan and Shugart (1989) and Price et al. (1999) because use of mean climate can introduce significant bias (e.g., Seastedt et al., 1994). For each stand, a stochastic climate record is generated for monthly temperature and precipitation using the spatially interpolated monthly means and standard deviations. Monthly temperature was assumed to be normally distributed. For monthly precipitation, a two parameter gamma distribution was used (Bratley et al., 1983). The shape and scaling parameters for the gamma distribution were:

$$\alpha = k \times \sqrt{\mu_P / \sigma_P} \text{ and } \beta = \mu_P / \alpha \quad \text{.......} (7)$$

where μ_P and σ_P are the mean and standard deviation, respectively, of monthly precipitation, and k is an empirically-derived multiplier equal to 1.7. Chapter 5 provides further details and illustrates that the method provides realistic long-term series. Precipitation estimates are increased by 10% to account for gauge undercatch (Bonan, 1988). Given the lack of variability data for solar radiation, mean monthly solar radiation is used for all simulations. The calculated climate is then used to calculate decay multipliers for soil temperature and moisture as detailed in the following section.

Abiotic multipliers

Soil moisture is calculated using the method of Parton et al. (1993, Appendix B). This is a simple water budget model operating on a monthly timestep which calculates the water content of each soil layer and saturated water flow between layers. Inputs are precipitation as rain or snow. Outputs are sublimation, evaporation, transpiration and losses to deep soil. The forest floor is defined as the upper soil layer with a depth as calculated by Equation 6. Successive layers in mineral soil are 15 cm thick to a maximum depth of 100 cm or to the soil depth recorded for the stand, whichever was lesser. Mineral soil is assumed to be uniform with a field capacity and wilting point as measured for the stand. Field capacity and wilting point of the forest floor (volumetric) are set to 19% (Goldring and Stanton, 1972) and 3.9% (Bonan, 1990a). Transpiration from each layer is weighted according to fractional root biomass in that layer using the logarithmic function described earlier (Equation 4) with a minimum of 0.1 to allow some access to deep soil water. For *P. banksiana*, transpiration is scaled by a factor of 0.5 because coniferous species in this region transpire at much lower rates than deciduous species relative to their foliage biomass (Sellers et al., 1997; Joiner et al., 1999; Baldocchi et al., 2000).

The PET algorithm of CENTURY, which is based on Linacre (1977), gave unrealistically high values in this study region. Rather than scale the output (e.g., Peng et al., 1998), the Jensen-Haise procedure is used (Jensen et al., 1990) following Bonan (1989) and Hogg (1994). This is based on a modified Priestly and Taylor (1972) formula. PET is calculated as a function of monthly mean solar radiation, monthly mean temperature and monthly mean minimum and maximum temperature of the warmest month. Winter PET is set to a minimum of 1 mm per month. Solar radiation is adjusted for slope and aspect as per Bonan (1989). This procedure provides realistic PET values in north American boreal forests (Bonan, 1988, Table 3.2)

Soil temperature in CENTURY is calculated using an empirical relationship between air and soil temperature. This relationship was developed for grasslands and consequently was judged unlikely to provide reasonable estimates of soil temperature in boreal forests where deep snowpacks and organic layers have substantial effects of heat flows. A simple alternative was formulated based on mean air temperature and one dimensional heat flow through a multi-layer soil. This routine operates on a daily timestep, where pseudo-daily temperatures and snowpack depths are generated from monthly mean temperatures and calculated snowpack depths using a thin plate smoothing spline (Press et al., 1986). The spline is iteratively adjusted to provide pseudo-daily values that reproduce input monthly means. The upper boundary condition is set by the calculated pseudo-daily air temperature, and the lower boundary condition is set by deep soil temperature which is taken to be equal to mean annual temperature plus 3 degrees (Briggs et al., 1989). For the purposes of the routine, soil is divided into a snow layer (if present), forest floor layer, and five mineral soil layers which are 0.2, 0.4, 0.6, 1.0 and 2.0 m thick. Thermal dynamics are calculated by numerical integration of the following equations for each day:

$$Q_{i-j} = \frac{0.0864 \times (T_i - T_j)}{\frac{D_i}{2 \times K_i} + \frac{D_j}{2 \times K_j}} \quad \text{.........(8)}$$

$$\Delta T_j = \frac{Q_{i-j} - Q_{j-k}}{D_j \times C_j} \quad \text{.........(9)}$$

where subscripts *i*, *j* and *k* denote successive soil layers, Q_{i-j} is the heat flux from layers *i* to *j* (W m^{-2} day^{-1}), T_i is the temperature of layer *i* (°K), D_i is the thickness of layer *i* (m), K_i is the thermal conductivity of layer *i* (W m^{-1} K^{-1}) and C_i is the heat capacity of layer *i* (MJ m^{-3} K^{-1}). For snow, forest floor and mineral soil layers, *K* values are 0.1, 0.2 and 1.2 W m^{-1} K^{-1} and *C* values are 0.5, 2.0 and 2.0 MJ m^{-3} K^{-1}, respectively (Oke, 1987, Table 2.1). Monthly mean temperatures of the forest floor and the upper mineral soil layer are calculated by averaging daily values for each month. Although this is a highly simplified model, it provides reasonable estimates of forest floor and mineral soil temperatures (see Validation section).

CENTURY decay routines utilize abiotic multipliers that scale decay rates as a function of soil temperature and moisture (Parton et al., 1993, Figure 2). Initial runs using these functions gave unrealistically low decay rates. A subsequent review revealed problems with both the temperature and moisture multiplier functions.

The temperature response function of CENTURY was parameterized from laboratory respiration data from cellulose at three temperatures, 10, 20 and 30 degrees (Sørensen, 1981; Parton et al., 1987). Clearly, many different functions could be fitted to three data points and there is no reason to suppose that the one used is applicable to boreal forests. This is of particular concern because boreal soil temperatures are below 10°C for most of the year and because the temperature response of fungi, which dominate boreal decomposition, is likely different to the laboratory incubations of Sørensen (1981). Consequently, the temperature function was reformulated as an Arrhenius type relationship using the model of Kätterer et al. (1998, Equation 1) with T_{ref} equal to 30°C.

$$T_{mult} = e^{\frac{E_a}{R}\left(\frac{1}{T_{ref}+273.15} - \frac{1}{T_s+273.15}\right)} \quad \text{.........(10)}$$

where T_{mult} is the temperature multiplier, E_a is the energy of activation (54800 J mol^{-1}), *R* is the universal gas constant (8.314 J mol^{-1} K^{-1}), and T_s is the soil temperature (°C). This relationship is illustrated in Figure 6-5.

The moisture response function of CENTURY relates the moisture multiplier to the ratio (H2030+PPT):PET where H2O30 is stored water in the top 30cm of soil, PPT is precipitation for the month and PET is potential evapotranspiration for the month. This index is unsatisfactory because it has no physical basis (e.g., it combines stocks and flows), its derivation has not been explained in the literature, and there is no rationale for applying it to a 2-layer system (forest floor and mineral soil). However, defining an alternative function is not straightforward. Data on moisture controls on decay rates are few, particularly for boreal conditions. Further, the literature data that do exist report short term responses to constant soil moisture. Extrapolation of these responses to monthly times scales is problematic because decomposers are responding to episodic precipitation events which result in fast wetting and slow drying, providing an extremely nonlinear response (e.g., Orchard and Cook, 1983, Figure 1) which is not easily averaged. A simple alternative function is proposed for CIOM in which it is assumed that activity is proportional to volumetric water content between field capacity and wilting point, which are the maximum and minimum water contents that can be returned by the water balance routine. Field capacity is taken to be optimal for microorganisms following Paustian and Schnurer (1987), with activity reducing to 20% at wilting point. Between field capacity and wilting point, a sigmoidal response curve as proposed by Bunnell and Tait (1974) is assumed (Figure 6-5) so that:

$$W_{mult} = 1/\left(1 + e^{P1*(P2-FAW)}\right) \tag{11}$$

where W_{mult} is the moisture multiplier, $P1$ and $P2$ are parameters set to 6.0 and 0.23 respectively, and FAW is fractional available water. This response is generally consistent with published moisture influences on forest floor and mineral soil respiration (Bunnell et al., 1977; Orchard and Cook, 1983; Linn and Doran, 1984; Bowden et al., 1998). This function does not consider saturating conditions, where activity can be reduced by restricted diffusion of oxygen, because the upland stands of this study were all well drained.

Temperature and moisture multipliers are calculated separately for forest floor and mineral soil, and for each layer the two multipliers are multiplicatively combined (Parton et al., 1993).

DECAY submodel

Decomposition

Litter is decayed using the algorithms and parameters of CENTURY 4.0 (Metherell et al., 1994) with the addition of organic layer slow and passive pools to allow the forest floor to be represented separately from mineral soil pools. These algorithms are implemented in the DECAY submodel and are briefly described below along with the modifications for this study. The submodel comprises a number of conceptual C pools (Figure 6-6) which undergo decay at different rates. Monthly surface and root litter inputs from the GROWTH submodel are each partitioned into an easily decomposed metabolic fraction, F_m, and a more resistant structural fraction. Metabolic and non-lignin structural fractions flow into an active pool, representing soil microbes and microbial products, then pass to a slow pool representing soil organic matter that is physically protected or chemically slow to decompose. The lignin fraction of litter does not create microbial biomass and directly enters the slow pool. A fraction of the slow pool passes to a passive pool which represents physically and chemically stabilized soil organic matter. Small fractions of the slow and passive pools are recycled to the active pools, representing decay in these two pools. Each transfer is accompanied by a loss of C to the atmosphere representing microbial respiration. Soil water carries soluble C from the forest floor active pool to the mineral soil active pool and thence into deeper layers or ground water, i.e., out of the system.

Carbon flow from each pool, i.e., decomposition, is equal to the C stock of that pool multiplied by a pool-specific maximum decay rate (see below), an abiotic multiplier representing the effects of temperature and moisture (see CLIMATE submodel), a mineral soil texture multiplier, T_m, (pool 3 only) and a lignin content multiplier, L_c, (structural pools only) (Parton et al., 1993). F_m, T_m and L_c are defined by:

$$F_m = \max\{0.2, \min(1 - L, 0.85 - 0.018 * L/N)\} \tag{12}$$

$$T_m = 1 - 0.75(1 - T_s) \tag{13}$$

$$L_c = e^{-3L_s} \tag{14}$$

where L is lignin fraction of litter, L/N is lignin:nitrogen ratio of litter, T_s is sand fraction of mineral soil and L_s is the fraction of structural material that is lignin. The pool-specific maximum decay rates are 4.9, 4.9, 7.3, 7.3, 18.5, 18.5, 0.2, 0.0045, 0.2 and 0.0045 year^{-1} for pools 1 to 10, respectively. The fraction of decomposition C lost to respiration for each pool, and the relationships for transfer of soluble C, are shown in Figure 6-6.

These parameters and relationships are taken from Parton et al. (1993) and Metherell et al. (1994). As noted earlier, however, this model differs from that of Parton et al. (1993) in that the forest floor is assumed to be physically separate from mineral soil and therefore has its own slow and passive pools. Parameters for these pools are assumed to be the same as mineral soil pools but without mineral soil texture effects.

Nitrogen cycling

Nitrogen stocks and transfers are calculated as per Parton et al. (1993) and Metherell et al. (1994). The N model has the same structure as Figure 6-6 but with the addition of a pool representing soil mineral N (NO_3^- and NH_4^+). Each C flow has an associated N flow, determined by the C:N ratio of the material being created which in most cases is a function of soil mineral N. C:N ratios of created material narrow as the availability of mineral N increases: as soil mineral N varies from 0 to 2 gN m^{-2}, C:N ratios vary linearly from 16 to 8 (pool 3), from 20 to 6 (pools 8 and 10) and from 40 to 12 (pools 7 and 9). The C:N ratio of flows from pool 4 to 9 is equal to 12 plus the C:N ratio of pool 4. The C:N ratio of flows into pool 4 varies linearly from 20 to 10 as the %N of surface litter (pools 1 and 5) varies from 0 to 2%. These C:N ratios, which are specific to forests, are taken from the study of Peng et al. (1998). The C:N ratio of structural material (pools 1 and 2) is assumed to be 150 with excess N being allocated to metabolic material (pools 2 and 6). Nitrogen associated with respired C is assumed to be mineralized. Atmospheric inputs and outputs are calculated from simple relationships (Parton et al., 1987; Parton et al., 1993):

$$N_{DEP} = 0.21 + 0.0028P_{ANN} \tag{15}$$

$$N_{FIX} = -0.18 + 0.014P_{ANN} \tag{16}$$

$$N_{VOL} = 0.02N_{GM} + 0.05N_{MIN} + 0.04N_{PL} \tag{17}$$

where N_{DEP} is atmospheric N deposition (gN m^{-2} yr^{-1}), N_{FIX} is symbiotic and non-symbiotic N fixation (gN m^{-2} yr^{-1}), P_{ANN} is annual precipitation (cm), N_{VOL} is N volatilization to the atmosphere (gN m^{-2} $month^{-1}$), N_{GM} is the gross N mineralization (gN m^{-2} $month^{-1}$), N_{MIN} is soil mineral N pool (gN m^{-2}) and N_{PL} is N in fresh plant litter (gN m^{-2}). Nitrogen may also be lost from the system by leaching, either associated with soluble C (see Figure 6-6) or as soluble N from the soil mineral N pool. The latter is given by:

$$N_{LEACH} = W_L / 18 * (0.2 + 0.7T_S) * N_{MIN} \quad \text{.......(18)}$$

where N_{LEACH} is gN m^{-2} $month^{-1}$, W_L is saturated water flow below 30 cm (cm $month^{-1}$) and T_S is fraction sand content.

Annual uptake of N by plants is the summation of C uptake of each vegetation component divided by its C:N ratio. Annual uptake is allocated to each month assuming uptake is proportional to monthly soil temperatures above zero. If uptake exceeds supply, it is limited to available supply and the excess demand is added to the demand of the next timestep.

Immobilization of N frequently occurs in the structural and metabolic pools. If there is insufficient soil mineral N for immobilization then decay may be limited by N availability. This limitation is represented by assuming that decay rates in these pools are reduced by a N multiplier (N_{MULT}) whose value is set by the Michalis-Menten relationship:

$$N_{MULT} = \min\{1.0, V_{\max} * N_{MIN} / (N_{MIN} + K_m)\} \quad \text{.......(19)}$$

where V_{max} and K_m are set to 1.1 and 0.1 gN m^{-2}, respectively.

Model implementation

Vegetation growth is updated annually, but litterfall is distributed across the 12 months as previously described. The CLIMATE and DECAY submodels operate on a monthly basis, although soil temperature calculation is done daily and decay routines use four timesteps per month for numerical integration. The model is run for two fire cycles of 75 years to initialize soil C pools, then is run for the required number of years to simulate each stand.

The model was implemented as a single run time file. It uses a separate input file for each stand which specifies stand name, species, latitude, elevation, slope and aspect, climatic variables, and soil variables (texture, depth, bulk density, field capacity and wilting point) as described previously. It also includes observed age and observed C density of trees, shrubs and forest floor for comparison with simulated values, as well as various initializing values which are necessary for the model to run but have insignificant effect on the output after two fire cycles. A separate file lists the stands to be simulated and defines length of simulation, fire cycles, outputs and various options, e.g., constant climate or stochastic climate. All parameters are specified in a third file. The model was written in FORTRAN77. When implemented on a 500 Mhz Pentium III PC, it runs 80 stands in about 45 minutes.

Sensitivity tests

The sensitivity of the model to a selection of input parameters was tested using the method of Friend (1993). The output variable was total forest floor C density (TFFC), which is equal to FFC plus rotten log C, at a stand age of 75 years for typical zone 1 stands of *P. banksiana* and *P. tremuloides*. Each selected parameter was varied by +/-10% and the index of sensitivity (β) calculated as:

$$\beta = \frac{(TFFC_1 - TFFC_0)/TFFC_0}{(P_1 - P_0)/P_0} \quad \text{.......(20)}$$

where $TFFC_1 = TFFC$ when parameter is P_1 and $TFFC_0 = TFFC$ when parameter is P_0. For parameters controlling vegetation growth, the calculated C pools at 75 years were varied by +/-10% rather than the underlying parameters. This simplified the analysis by combining the effects of multiple parameters. Similarly, the sensitivity to potential evapotranspiration (PET) was tested by varying PET by +/- 10%.

In addition, the sensitivity of *TFFC* to several assumptions was tested by altering these assumptions and calculating the percent change in *TFFC*.

Model validation

To provide a degree of confidence that CIOM was providing realistic simulations, a variety of outputs were compared against literature data with the model run for comparable conditions. Carbon stocks, litterfall, soil respiration, temperature and moisture, and transpiration were validated primarily against data from BOREAS studies. Climatic and soil data for these comparisons were taken from chronosequence stands that were co-located or close to the BOREAS sites being compared.

To validate decay rates, simulated mass remaining was compared with the results of two recent Canadian litter bag experiments (Taylor et al., 1991; Moore et al., 1999). For this purpose, the model was modified to track decay of a single 100 g m^{-2} pulse of foliage litter over three years, applying forest floor environmental conditions that were derived from a prior run of the model. It was assumed that there was no plant uptake of nitrogen, i.e., no roots grow into the litter bag. The study of Taylor (1991) was for Kananaskis in southern Alberta, which has been termed climatic zone 4 for convenience; climatic data were taken from the Kananaskis climate station.

Validation of forest floor C:N ratio was done by comparing measurements from chronosequence stands to simulations for those stands; the observed C:N ratios were derived from a subset of forest floor field samples as part of measurements taken to determine LOI-Organic C relationships (Nalder and Wein, 1999). To validate the soil nitrogen budget, various literature data were compared with simulated soil inputs and outputs at a stand age of 50 years. Simulations were carried out for both species in each of three zones, using the six stand input files developed for the dynamics runs (see Forest Floor Dynamics section below).

To validate overall operation of the model, mineral soil C and forest floor detrital C were predicted for 21 *P. banksiana* and 47 *P. tremuloides* sites taken from the database of Siltanen et al. (1997). For this purpose, sites were selected that were within 200 km of Prince Albert, Fort

Smith, and Thompson, i.e., overlapping with zones 1, 2 and 3 of this study. Data were extracted from the database for mineral soil C density to a depth of 20 cm (interpolating between horizons where necessary), C density of the LFH layer, and percent silt and percent clay of the mineral soil. Field capacity and wilting point were assigned based on soil texture. Climatic data for each site were typical data for the zone in which the site was located. In the absence of any data on composition or age, it was assumed that each site was mono-specific and that a stand-replacing fire had occurred 50 years ago. The final validation compared simulated FFC density for each of the 80 chronosequence stands with observed values previously reported in Nalder and Wein (1999).

Forest floor dynamics

After validating the model, runs were carried out to examine long-term forest floor dynamics and to explain differences between species and among climatic zones. The output variable was FFC. For this purpose, input stand files were generated using latitude, elevation and climatic data from Prince Albert, Fort Smith and Thompson to represent zones 1, 2 and 3, respectively, and using common soil conditions that were typical of a sandy loam soil. The runs for zone 1 were also used to examine the dynamics of each forest floor C pool and each component of litter input to the forest floor.

Results and Discussion

Sensitivity

CIOM is a input-output model that seeks to explain long-term forest floor dynamics in the upland forests of the western boreal. To aid interpretation, the model is as simple as possible consistent with realistically representing litter inputs and C outputs from decay at an annual timestep. All parameters were independently derived from published field data or from well-validated models or from the chronosequence field data of this study. As is common in forest models, many parameters are not accurately known, but CIOM proved insensitive to changes in most parameters and key variables (Figure 6-7). Index of sensitivity values (β) were generally less than 0.3, indicating low sensitivity. Sensitivities were similar for both species. The model was also fairly insensitive to changes in assumptions (Table 6-5). The lack of sensitivity of CIOM to a wide range of parameters and assumptions provides confidence that even if these are not precisely defined, the likely errors in calculating forest floor C will be small.

Two of the 45 sensitivity tests, however, had β values above 0.5. These were the energy of activation (*E*a) parameter defining the temperature multiplier function and the maximum decay rate parameter of the forest floor slow pool. The first is derived from an extensive data set (Kätterer et al., 1998), and the second is well-validated (e.g., Parton et al., 1987; Parton et al., 1993; Vitousek et al., 1994; Peng et al., 1998) so were considered unlikely to be significant sources of error.

The model was also slightly sensitive to four other parameters (forest floor field capacity, root distribution coefficient, and foliage and fine root retention times), and two variables (tree foliage growth and fine root growth). Of these, foliage retention time for *P. banksiana* as well as root retention times for both species are poorly known and therefore could lead to significant bias in the model output. As noted earlier, the foliage retention time for

P. banksiana was estimated as four years from BOREAS needle age studies (Gower et al., 1997). The literature, however, indicates other values may be appropriate. Other simulations have used 2 years (Table 3 Bonan, 1990b) and 3 years (MacLean and Wein, 1980). A similar species, *Pinus contorta*, has foliage retention times ranging from 5 to 18 years (Schoette, 1990) indicating that values higher than 4 years may also be appropriate. Nevertheless, the close agreement between observed and simulated litterfall data (Table 6-6) indicates that the chosen value of foliage retention time is realistic.

Uncertainty also surrounds the appropriate value for fine root retention time. The model uses a value of 2 years, equivalent to a fine root turnover 0.5 yr^{-1}. Kurz et al. (1996) reviewed root production data and estimated fine root turnover to be 0.735 yr^{-1} for Canadian forests, but NPP simulations with the CBM-CFS2 model have suggested a value of 0.5 $^{yr-1}$ may be more appropriate for Canadian boreal forests (Li et al., 2002). A review of EuroSiberian boreal forests noted great variability, but suggested a value of 1 yr^{-1} (Schulze et al., 1999). For specific sites, Ruess et al. (1996, Table 3) measured a value of 0.33 yr^{-1} in an aspen-birch stand in interior Alaska, and Steele et al. (1997, Figure 8) measured values from 1.4 to 1.8 yr^{-1} in *P. banksiana* and *P. tremuloides* stands in BOREAS SSA and NSA. Clearly there is considerable uncertainty surrounding this parameter. Nevertheless, the value used here seems reasonable based on BOREAS root litter measurements. CIOM estimated fine root litter in the top 30 cm of soil profile to be 79, 92, 77 and 92 gC m^{-2} yr^{-1} for the SSA-OA, NSA-OA, SSA-OJP and NSA-OJP sites, respectively. For the same sites, fine root NPP is estimated as 29, 44, 105 and 95 gC m^{-2} (from data in Figure 8 Steele et al., 1997), which on the assumption that fine root litter was at equilibrium, gives comparable litter input to that simulated, lending support for the chosen value of fine root retention time.

Validation

Simulated total C stocks were generally in line with observed values (Figure 6-8), although there were some large discrepancies between some components, e.g., simulated stem C density for young jack pine sites is about twice that observed. Rather than reflecting on the realism of the model, however, these differences are more likely caused by sampling variability, variability among stands within a zone, and perhaps BOREAS sites being atypical of stands of that age in that region.

Litterfall is notoriously variable making comparisons with simulations difficult. Nevertheless, the model provides estimates of aboveground litterfall that are close to observed at BOREAS intensive study sites and other sites in the western Canadian boreal forest (Table 6-6). Simulations also reflect observed differences between species and between southern and northern regions of the western boreal. Root litter is also a major input to the forest floor, but no suitable observed data were available for comparison. Boles can be another important source of litter (see Forest Floor Dynamics section). Over time, boles are incorporated into the forest floor as rotten logs (Nalder and Wein, 1999). Figure 6-9 compares the observed pattern of rotten log dynamics for the chronosequence stands with equivalently derived data from simulations of the same stands. The simulations provide similar overall amounts of rotten log C, as well as reflecting the small differences between species. The dynamics, however, are quite different to that observed, with the simulations showing initial peaks coming much earlier in a stand life. The reason for this is unclear, but may be due to difficulties in the field in assessing whether a log has been incorporated into the forest floor. Alternatively, the model parameters for snag breakdown may be in error. However, simulated snag C for each of the 80 stands gave means of 0.40 and 0.34

kgC m^{-2} for *P. banksiana* and *P. tremuloides* stands, respectively, which is close to observed means of 0.32 and 0.55 kgC m^{-2}, indicating that the snag parameters are reasonable.

Simulated soil respiration is compared with observed data in Table 6-7. For the BOREAS sites, simulated values are lower than observed, particularly in summer, but this is to be expected as the model does not simulate root respiration. Root respiration can be a large part of total soil respiration (Buchmann, 2000; Hanson et al., 2000, Table 1; Sawamoto et al., 2000; Widen and Majdi, 2001) which is borne out by the data in Table 6-7 (e.g., compare undisturbed and clear-cut areas for the SSA-OJP site, or root and microbial respiration in Finland Mixed site). Russell and Voroney (1998) suggest root respiration accounts for 60% of total soil respiration for the SSA-OA site. Making allowances for the likely additional contributions from roots, the simulated data are consistent in magnitude with observed. They also reflect the differences between species and between winter minimums and summer maximums that are evident in the observed data.

Simulated seasonal soil temperatures were very close to that measured at the BOREAS SSA-OA site (Table 6-8) indicating that the soil temperature calculations were providing realistic values. May to August air temperatures in 1994 were slightly cooler than long-term averages while September was 3 degrees warmer (Russell and Voroney, 1998, Table 1) which tend to account for the small differences between observed and simulated soil temperatures. Simulated soil moisture values were generally lower and more constant than observed values, but this would be partially due to the pattern of precipitation in 1994: compared with long-term averages, precipitation in 1994 was much higher in May and June and lower thereafter (Russell and Voroney, 1998, Table 1).

Simulated transpiration and evapotranspiration for selected BOREAS sites were generally close to observed values for 1994 (Table 6-9), both in magnitude and seasonal patterns. Observed transpiration for SSA-OA site was somewhat higher than simulated using long-term climate averages, but again this may be due to the higher than average precipitation in 1994 (Russell and Voroney, 1998, Table 1).

For litter bag decay, simulated mass remaining after three years reflects the trends evident in data from two recent Canadian field studies (Taylor et al., 1991; Moore et al., 1999): for both data sets, mass remaining was less (faster decay) in zones 1 and 4 than in 2 and 3, and *P. tremuloides* had lower mass remaining than *P. banksiana* (Table 6-10). However, simulated mass remaining was, with one exception, lower than observed, particularly for *P. tremuloides*, which may cast doubt on the model's decay rates. It is likely that at least part of the discrepancy is due to uncertainty in the modelled N cycle, which is particularly critical in the first year of decay when immobilization occurs. For instance, removing 0.75 gN m^{-2} yr^{-1} from the annual N budget for *P. tremuloides* in zone 1 changed the simulated mass remaining from 44% to 62%, with the increase being due to N limitations on decay. As noted below, the soil N budget is not well known and it is possible that medium term litter bag experiments are undergoing N limitations that the model cannot capture. The discrepancy may also be due to the fact that litter bags in the field are exposed to more extreme microclimate than the underlying forest floor, particularly moisture regime, which may tend to limit decay rates.

There was reasonably good agreement between observed and simulated C:N ratios (Figure 6-10). Both observed and simulated show *P. banksiana* consistently had wider ratios than *P. tremuloides*. Some observed *P. banksiana* ratios were somewhat higher than simulated.

The reason for this is unknown, but it should be noted that the presence or absence of an alder understory in *P. banksiana* can have a substantial effect on C:N ratios (Vogel and Gower, 1998); such effects are not simulated by CIOM as it does not distinguish between species of shrubs.

Simulated nitrogen budget data are presented in Table 6-11. The realism of each component is discussed in the following subparagraphs:

(a) Mineral nitrogen pools vary by zone and species. Unfortunately, there is a paucity of data for comparison. For *P. banksiana*, MacLean and Wein (1977, Table 6) reported a mean of 3.81 gN m^{-2} in New Brunswick and Foster and Morrison (1976, Table 7) reported 2.9 gN m^{-2} in central Ontario. However, both sets of measurements were taken in August when mineral nitrogen levels may be peaking (e.g., Stottlemyer and Toczydlowski, 1999, Figure 4) which would tend to explain the lower simulated values for annual means. No comparable data were available for *P. tremuloides*.

(b) For nitrogen mineralization the only comparable data are for *P. tremuloides*: stands in interior Alaska have forest floor mineralization rates of 4.3 and 4.5 gN m^{-2} yr^{-1} (Flanagan and van Cleve, 1983, Table 5). These data are in line with the simulated values for zone 2, which has a similar temperature and moisture regime, given that simulated values include mineralization in the top 20 cm of mineral soil in addition to the forest floor. In the Alaskan studies, conifers had lower mineralization rates than *P. tremuloides* (van Cleve and Yarie, 1986, Figure 12.10) which also occurs in the simulated values.

(c) Simulated nitrogen deposition values were close to what would be expected. Deposition generally decreases moving north and west across the Canadian boreal forest (Brydges, 1998, Figure 1; Chen et al., 2000b, Figure 7). Values of 0.63, 0.76. and 0.21 gN m^{-2} yr^{-1} have been reported in Minnesota (Alban et al., 1978, Tables 4 and 5), central Ontario (Foster and Morrison, 1976, Figure 1) and central Alaska (van Cleve et al., 1983, Table 8), respectively, which bracket the simulated values of 0.32 to 0.38 gN m^{-2} yr^{-1}. Additionally, Huang and Schoenau (1997, Table 3) reported a value of 0.27 gN m^{-2} in the BOREAS SSA from May to October 1995, which is consistent with simulated annual values for zone 1.

(d) Simulated nitrogen fixation ranged from 0.40-0.69 gN m^{-2} yr^{-1}. Observed data span a much wider range. Wei and Kimmins (1998, Figure 1) estimated asymbiotic nitrogen fixation as 0.08 gN m^{-2} yr^{-1} from woody debris in pine stands in interior British Columbia. At the other extreme, Klingensmith and van Cleve (1993) estimated symbiotic inputs of 16.4 gN m^{-2} yr^{-1} in early succession alder in Alaska. Laboratory incubations of *P. tremuloides* soil at 25 °C for a range of amendments give asymbiotic fixation rates between 0.35 and 3.25 gN m^{-2} yr^{-1} (Brouzes et al., 1969); considering that soil temperatures in the western boreal are much lower, these data would be consistent with simulated values. An upland aspen-birch stand in interior Alaska has total nitrogen fixation of 0.4 gN m^{-2} yr^{-1} (Ruess et al., 1996, Table 4) which is also in line with simulated values here. However, simulations for the SSA-OA site with the detailed process-based model *ecosys* estimated asymbiotic N fixation as 2.0 gN m^{-2} yr^{-1} (Grant and Nalder, 2000), which is much higher than CIOM estimates. Also, many stands in this study had a significant understory of alder (*Alnus crispa*), most had some *Sherperdia canadensis*, another nitrogen-fixing shrub, and the amount of woody debris varied widely. Consequently, it is possible that actual nitrogen-fixation rates could vary considerably from simulated values.

(e) The only comparable data for leaching losses come from interior Alaska, where leaching losses in an aspen stand are 0.07 gN m^{-2} yr^{-1} (van Cleve et al., 1983, Table 8). This may indicate that simulated values are high.

(f) Simulated plant uptake of nitrogen appears reasonable and values are consistent with literature data. In the BOREAS SSA and NSA, the aboveground overstory of *P. banksiana* stands take up 0.6 to 1.7 gN m^{-2} yr^{-1} with SSA stands being higher (Vogel and Gower, 1998, Figure 3). In northern Ontario, aboveground uptake in mature *P. banksiana* stands is 3.2 gN m^{-2} yr^{-1} (Foster and Morrison, 1976, Figure 1). In interior Alaska, uptake over a range of species is 0.42 to 7.91 gN m^{-2} yr^{-1} with *P. tremuloides* near the upper end of this range.

(g) No comparable data could be found for nitrogen volatilization. However, Klingensmith and van Cleve (1993) found very low to undetectable levels of denitrification in a floodplain successional sequence in interior Alaska; denitrification could be expected to be lower in upland stands with lower moisture contents, suggesting that the simulated values may be high.

In summary, comparable field data for mineral nitrogen cycling are few. Those that do exist do not invalidate the simulated values, but at the same time, they are insufficient to provide a high confidence in the simulated data.

Mean simulated mineral soil C for the 68 sites from Siltanen et al. (1997) was 2.74 kgC m^{-2} which was close to observed mean of 2.42 kgC m^{-2}. Given the approximations used for the simulation, there was also a reasonably close relationship between simulated and observed values (R^2=0.39). The mean simulated detrital forest floor C for these sites was 2.39 kgC m^{-2} which was also close to observed value of 2.25 kgC m^{-2}. These close agreements indicated that CIOM was correctly representing the balance between C inputs and outputs for both mineral soil and forest floor pools.

For the 80 chronosequence stands of this study, simulated and observed values of FFC are presented in Figure 6-11. Simulated values are of the same general magnitude as observed, again indicating that CIOM is able to approximate FFC dynamics. As expected, the model does not reproduce the considerable scatter evident in the observed data; much of this scatter is undoubtedly due to natural and sampling variability (e.g., Nalder and Wein, 1998a) rather than reflecting differences in climate or soil. For *P. tremuloides*, there is good agreement between observed and simulated, although the model overestimates FFC in zone 3. The model reflects the observed differences between species, with *P. tremuloides* generally having higher FFC than *P. banksiana*. There was, however, a tendency for the model to overestimate FFC for *P. banksiana*. There are a number of possibilities for this. First, observed data may underestimate true accumulation rates because the possibility of undetected, post-establishment surface fires which can remove some of the forest floor. Although considered unlikely because of the care taken to exclude stands with any signs of post-establishment fires, it cannot be completely ruled out. Second, the observed data excluded concentrations of forest floor materials, such as squirrel middens, which would not be excluded by the model. This is not, however, a large component: on average these would add 30 gC m^{-2} to FFC (Nalder and Wein, 1999). Third, FFC in *P. banksiana* stands is related to moss dominance; moss-dominated stands have more FFC than those dominated by lichen (Nalder and Wein, 1999, Figure 8). No attempt was made to distinguish between moss and lichen in CIOM because there were inadequate data to parameterize such a distinction (Nalder and Wein, 1999). Consequently, moss dominance effects are not captured, and this may lead to discrepancies in stands that are lichen-dominated. Fourth, the model does not simulate individual shrub species, but it appears that the N-fixing shrub *Alnus crispa* may have an effect on FFC, e.g., in the *P. tremuloides* stands, 13 of the 25 that were overestimated had the understory dominated by *A. crispa*, compared with only 4 of the 20 that were underestimated. This may be due to N fixation alleviating N limitations on decomposition. Alternatively, low C:N alder leaves have been reported to promote faster forest floor decomposition, possibly through increases in soil faunal activity (Prescott96a). It is also possible that the conditions that promote alder growth, such as a moister microclimate, also favour higher rates of decomposition. On the other hand, Vogel and Gower (1998) report higher forest floor C density in alder-dominated stands of *P. banksiana*. Fifth, given the uncertainty in the N budget, it is possible that CIOM is overestimating N limitations for *P. banksiana*. However, this effect is relatively small, e.g., adding 1 gN m^{-2} yr^{-1} to the annual N budget for simulations of the chronosequence *P. banksiana* stands essentially removed the N limitation but only reduced mean FFC by 5, 8 and 12% for zones 1, 2 and 3, respectively. On balance, the overestimates are likely due to a combination of factors rather than revealing any inherent problem with the model.

In summary, this extensive set of validation tests suggests that the model is reasonably simulating inputs and outputs. Simulated values for C stocks, litter, soil temperature, soil moisture, transpiration and C:N ratios were all consistent with comparable observed data. Simulated N inputs and outputs appear reasonable, although this is a difficult area for comparison due to the paucity of observed data. Simulated 3-year decay rates were somewhat higher than observed in litter bag studies, but this does not invalidate the model for long-term studies. There was good agreement between observed and simulated means of mineral soil C and total forest floor C for 68 independent sites across the western boreal, indicating that on average the litter and decay routines are correctly representing C flows. There were, however, some discrepancies between simulated and observed FFC for the 80 chronosequence stands. These discrepancies raise some questions, but are not serious enough to invalidate the model. Based on the sensitivity and validation tests, CIOM was judged adequate for its primary purpose, which is interpreting forest floor dynamics and identifying areas for further research.

Forest floor dynamics

Figure 6-12a shows the simulated long-term FFC dynamics for each species and zone. These predictions clearly show a long-term increase in FFC for both species. There was a substantial difference between species, but no consistent differences among zones. It can also be seen from Figure 6-12 that FFC dynamics are largely a reflection of litter dynamics. FFC increases rapidly in the first couple of decades when litter input is high then at a much slower rate as litter input stabilizes. As with FFC, litter inputs show substantial differences between species, but minimal differences among zones. These relationships highlight the importance of litter inputs in defining forest floor dynamics.

Litter, however, presents a complex picture. Inputs varied not only over time (Figure 6-12b) but also in composition (Figure 6-14). Logs formed the largest component during the first 1-2 decades and continued to form a substantial input thereafter. The first pulse of log litter is derived from trees of the previous stand which are killed by the stand-replacing fire. These snags breakdown over time to form logs (coarse woody debris), then finally enter the forest floor as rotten log litter. Following the first pulse of log litter in the first couple of decades, foliage litter became the largest component. For *P. banksiana*, however, moss-plus-lichen litter was the largest component after about a 100 years. This was surprisingly large, but should be realistic. Moss-plus-lichen C stocks were well defined given the high R^2 of the regression (Table 6-2) and the annual mortality parameter (=20.4%) does not seem unreasonable. It should be noted, however, that this parameter was derived for moss, and lichen may produce less litter than moss (Ipatov and Tarkhova, 1983); even if this parameter is halved, however, it does not make a large difference to FFC, only reducing mean FFC reported in Figure 6-11 by 10, 14, and 11% for zones 1, 2 and 3, respectively. For both species, fine roots formed the next largest source of litter input. Branch litter from self-pruning formed a substantial input in early stages, then declined as the stand aged. It should be noted that branch litter may be slightly underestimated as it considers only self-pruning, not other branch mortality, but being a small component, this is probably not important. The next component, shrub litter, was negligible for *P. banksiana* but made a small contribution for *P. tremuloides*. It might have been expected that *P. tremuloides* shrub litter would be a larger component given the results from the BOREAS SSA-OA site, where shrub leaf area index exceeded that of trees for much of the 1994 growing season (Black et al., 1996). The SSA-OA site, however, had a very dense shrub layer that was atypical of those sampled for the chronosequences in this study. For both species, coarse root litter was a small component, except for the first year when there was a large pulse from trees killed by the stand-replacing fire. In summary, components of litter C vary considerably in importance with stand age and species. None of the components simulated can be ignored, and for some, there is a need to confirm or improve parameters for future modelling.

Forest floor dynamics are also affected by the various forest floor C pools and their outputs. To illustrate, the dynamics of each pool for zone 1 are presented in Figure 6-13. For both species, the slow C pool was the major component and as such its maximum decay rate parameter forms a major control on FFC; this was confirmed by the sensitivity analysis (Figure 6-7). The structural pool was a significant component in the first decade, but declined in relative importance thereafter. Metabolic, active and passive pools are relatively unimportant as C stores. Roots also formed a significant part of FFC, increasing with stand age as the forest floor deepens. Carbon outputs are determined by the C stocks of each detrital pool multiplied by its maximum decay rate parameter modified by the temperature, moisture and nitrogen multipliers. For these runs, the main decay rate modifier was the temperature multiplier; values were low and exhibited significant interzonal differences (Table 6-12). Values of the nitrogen multiplier showed inter-zonal and inter-species differences, but were relatively high and therefore had only a small effect on decay rates. Moisture multiplier values were all close to 1.0 and had very little effect on decay rates. In summary, the most important controls on forest floor C outputs are the maximum decay rate parameter of the slow pool and the temperature multiplier.

Three hypotheses were raised at the start of the wider study into forest floor dynamics (Nalder and Wein, 1999). The first hypothesis, that there is a long-term accumulation of FFC over the life of a stand, is supported by the model predictions. For both species in each of the three climatic zones, FFC continued to increase over the 150 simulation years, although the rate of increase was lower after the first couple of decades (Figure 6-12a). Given the results from the chronosequence field studies, as well as indications from published literature (Nalder and Wein, 1999), these increases were expected for *P. tremuloides* but were a surprise for *P. banksiana*. According to outputs from CIOM, the long-term increase in FFC is primarily a consequence of increases in the slow pool (Figure 6-13), aided by moderate increases in annual litter input after the first few decades (Figure 6-14). Inputs and outputs for the slow pool for the last year of simulation in Figure 6-13 were 55.7 and 48.0 gC m^{-2} yr^{-1} for *P. banksiana* and 72.3 and 68.2 gC m^{-2} yr^{-1} for *P. tremuloides*, suggesting that the slow pool would continue to increase. Of course, the model is not parameterized for longer periods, nor do stands often survive for this period in the region studied. Nevertheless, forest floor accumulations more than a metre deep have been reported on fire protected islands in the Swedish boreal forest (Bradshaw and Zackrisson, 1990; Berg and Ekbohm, 1993), so given the right conditions, FFC accumulations over much longer periods may also be realistic.

The second hypothesis, that there is a difference in FFC between species, was also borne out by the predictions: throughout the 150 simulation years, *P. tremuloides* FFC was substantially higher than that for *P. banksiana* (Figure 6-12a). This was not a surprise. The same result was obtained from the chronosequence field study and species differences are commonly found in the literature (Nalder and Wein, 1999). The model shows that this is primarily due to higher litter input rates for *P. tremuloides* (Figure 6-12b). Foliage litter input, in particular, is nearly twice that of *P. banksiana* (Figure 6-14); this is to be expected since both species carry similar foliage biomass (e.g., Gower et al., 1997), but in common with other conifers, *P. banksiana* has a longer foliage retention time than the deciduous *P. tremuloides*. Another factor contributing to the higher FFC for *P. tremuloides* is that its temperature multiplier is lower (Table 6-12) contributing to lower decay rates. The lower temperature multiplier occurs because the forest floor of *P. tremuloides* is deeper, which provides more insulation and lowers summer soil temperatures. The differences, however, are mitigated by differences in litter quality, mainly lignin fraction. Although FFC was only slightly sensitive to lignin fraction (Figure 6-7), there are large differences in lignin content between the two species (Table 6-4). These differences can have a substantial effect on FFC. For instance, swapping litter lignin parameters between species in zone 1 results in *P. banksiana* FFC declining by 19% and *P. tremuloides* FFC increasing by 27%. This occurs because higher lignin fractions result in more structural C (Equation 12); structural C has a slower decay rate than metabolic C, and loses less C to respiration because of the fraction going directly to the slow pool which has a low respiration loss (Figure 6-6).

The third hypothesis was that there would also be differences in FFC among climatic zones. It was expected that this hypothesis would be supported. First, the climatic zones used in this study vary considerably, with mean annual temperature ranging from –0.2 °C to –3.9°C and mean annual precipitation ranging from 385 mm to 508 mm (Table 6-1). Second, the chronosequence field studies had found a strong effect of climate, at least for *P. tremuloides* (Nalder and Wein, 1999). There was, however, no evidence in simulated FFC of significant differences among zones for either species: while differences did occur, they were generally small, were not consistent for each species and the patterns varied over the 150 simulation years. The literature reviewed by Nalder and Wein (1999) also provided an ambiguous picture. Since low soil temperatures and low soil moisture are limiting on decay (Bunnell et al., 1977), it had been thought that the range of climate would produce zonal differences in FFC. According to CIOM outputs, this does not occur for two reasons. First, moisture is not often limiting – when the moisture multiplier is averaged over 150 years, it is close to 1.0 in all cases (Table 6-12). Second, although differences in temperature lead to substantial differences in the temperature multiplier, this is offset by changes in productivity and litterfall, e.g., for *P. tremuloides*, the temperature multiplier averaged over 150 years is 23% higher in zone 1 than 3 (Table 6-12), but this is offset by 22% higher litterfall in zone 1 (Figure 6-12) due to higher productivity in the warmer climate (see coefficients in Table 6-2). In summary, evidence for a climatic effect on FFC is conflicting – further study will be required to resolve this issue.

Despite the lack of simulated climatic effects, CIOM outputs do suggest that climate change may impact forest floor C storage in the western boreal. It must be borne in mind that the model can provide limited guidance because it does not account for factors such as CO_2 fertilisation and its impacts on litter quality, and some concerns remain about the model's accuracy. Nevertheless, the model is useful to illustrate the potential for change. Based on the results reported here, which support the first two hypotheses, there are two main mechanisms by which a changing climate may alter forest floor C storage. First, the long-term FFC accumulation suggests that forest floor C storage will be sensitive to disturbance intervals. Fire regimes in particular have historically been sensitive to climate (Clark, 1988; Bradshaw and Zackrisson, 1990; Clark, 1990; Bergeron and Flannigan, 1995; Larsen, 1997) and are expected to change considerably under climate change scenarios (see review in Weber and Flannigan, 1997). Annual area burned is expected to increase substantially in western Canada for climate change scenarios (Amiro et al., 2001). Such changes will alter the average age of stands and therefore change FFC storage across the landscape. For example, based on the zone 1 dynamics of FFC in Figure 6-12a, a reduction of average stand age from 75 to 50 years would reduce mean FFC by 19% and 12% for *P. banksiana* and *P. tremuloides*, respectively. Second, shifts in the distribution of species have been hypothesized or predicted to occur as a result of climate change (Pastor and Post, 1988; Wein, 1990; Landhäusser and Wein, 1993; Hogg, 1994; Burton and Cumming, 1995; Thompson et al., 1998), and in western Canada, dramatic changes in the distribution of *P. banksiana* and *P. tremuloides* are predicted by the Canadian Climate-Vegetation Model for a doubled CO_2 climate (Lenihan and Neilson, 1995). Based on the predictions in Figure 6-12a for zone 1, replacement of *P. tremuloides* by *P. banksiana* would reduce mean FFC by 38% assuming an average stand age of 75 years. Conversely, replacement of *P. banksiana* by *P. tremuloides* would increase mean FFC by 62%. Clearly the potential exists for a changing climate to substantially alter forest floor C storage in upland forests of the western boreal.

Future work

One of the important applications of models is to identify unknowns and pin-point areas for future research. CIOM has highlighted many uncertainties and areas for improvement. To begin with, the GROWTH submodel is based on empirically derived relationships for defining vegetation C stocks and litterfall. Consequently, it is very limited in application because it cannot be used outside its parameterization limits, it cannot be fully coupled to soil processes, especially at high temporal resolutions, and it cannot represent many effects such as CO_2 fertilization which may be important in climate change studies. Future modelling work should include physiologically-based vegetation growth to explicitly represent the processes of photosynthesis, respiration and allocation. The use of conventional patch models has been ruled out in previous work (Chapter 5), but there are still many possible approaches operating at different temporal resolutions, e.g., *ecosys* (Grant et al., 1999), FINNFOR (Kellomäki et al., 1993; Kellomäki and Väisänen, 1997; Venalainen et al., 2001), TEM (McGuire et al., 1995), or HYBRID (Friend et al., 1993). All would require some parameterization for upland species in the western boreal, but this should be possible given the availability of data from BOREAS and the chronosequences studied here.

The value of such a model is still constrained, however, by the lack of data in four key areas. First is the lack of data on forest floor litter inputs from logs and fine roots. Regardless of the model's methods of calculating these variables, data are needed to validate and constrain these calculations. Detailed studies of the dynamics of snags and logs, including aboveground decay rates, are required for upland species in the western boreal. Research into dead wood in the western boreal has so far concentrated on fine woody debris because of its importance as fuel for forest fires (e.g., Nalder et al., 1999), but coarse woody debris has been little studied. There is also a paucity of fine root biomass, turnover and decay data, although mini-rhizotron studies are providing promising results (e.g., Steele et al., 1997; Tierney and Fahey, 2001) and may soon fill many of these gaps. Second, moss-plus-lichen is an important litter source in *P. banksiana* stands, but the controls on whether moss or lichen are dominant need to be determined. Also more data are required to confirm the litter mortality parameter used here, particularly for lichen dominated stands. Third, N budgets in the western boreal are uncertain. Nitrogen is frequently cited as limiting growth in boreal forests, and as shown by simulations here, it can be a control on litter decay. Detailed N budget studies are needed to measure inputs and outputs, particularly N fixation, and to obtain seasonal measurements of soil mineral N for model validation. Fourth, shrubs can play an important role, not only by contributing to litter and influencing litter quality but also by fixing N and altering the N budget. For instance, alder has been shown to influence growth (Vogel and Gower, 1998) and decay (Prescott, 1996), and indications from this study that *A. crispa* affects FFC are confirmed by the study of Vogel and Gower (1998). It is less clear, however, what mechanisms control the establishment and growth of major shrub species, such as *A. crispa* and *Corylus cornuta*, in the western boreal. It is suspected that shrubs are opportunistic (Nalder and Wein, 1999), but a better understanding of the controls is required to be able to model them.

Another area requiring more study is the appropriateness of maximum decay rate parameters for the forest floor C pools. Following Vitousek et al. (1994), CIOM assumes that these parameters, which were originally derived for organic matter in mineral soil, would apply to the organic layer by setting mineral soil texture effects to zero. Vitousek et al. (1994) achieved reasonable results for 2-year mass loss of leaves for an altitudinal gradient in Hawaii, but the applicability to boreal conditions is questionable in view of several concerns raised by this study. The first concern is that simulated 3-year litter bag decay for a range of climate within the western boreal consistently gave lower residual mass than those predicted from field studies (Table 6-10). This may indicate that the model decay rates are too high, at least in the short-term. The second concern, given the general underestimates of FFC for *P. banksiana*, relates to the appropriate decay rate for the slow pool which dominates long-term dynamics (Figure 6-13). It has been reported that pine foliage (*Pinus contorta* and *Pinus sylvestris*) exhibits a different pattern of mass loss to deciduous species (*Betula pubescens* and *Alnus incana*), being slower in the first two years, reaching similar values from 2-3 years, then being greater thereafter (Berg and Ekbohm, 1991; Berg et al., 1995). In contrast, CIOM predicts the same pattern for *P. banksiana* and *P. tremuloides*, with *P. banksiana* having the lowest mass loss in the long-term (Figure 6-15). In the longer term, the regression model of Berg and Ekbohm (1991) indicates that pine litter mass loss reaches an asymptote of 80-100% compared with 51% for *Alnus incana* and 54-56% for *Betula pubescens*. Similar differences between pine and deciduous species have been observed in subsequent studies (Berg et al., 1996; Berg, 2000; Berg et al., 2001). If a similar pattern applied to *P. banksiana* and *P. tremuloides*, this would account for the low levels of FFC observed in *P. banksiana* stands relative to *P. tremuloides*. As a result of these concerns, some doubt must remain about the appropriateness of C pool decay parameters used in CIOM. Longer term data from the CIDET experiment, which is scheduled to run for 10 years (Trofymow et al., 1995), will be invaluable for resolving this issue.

It will not be possible, however, to resolve these concerns without confirmation of the abiotic multipliers. CIOM was sensitive to the temperature multiplier function (see energy of activation parameter in Figure 6-7a) which is a concern because there is some doubt regarding the appropriate function. For example, some other decomposition temperature response functions vary significantly from the one of Kätterer et. al (1998) used in CIOM (Figure 6-16), particularly at temperatures below 15 degrees which is the range of interest in the western boreal (see Table 6-8). The difficulty is that few, if any, low temperature data were used in deriving each of these functions. The one used here was based on the most extensive data set (86 incubations), but even then only three data points were below 5 °C.

A further concern is raised by research in Finland which found that decay of old soil organic matter had a lower temperature sensitivity than that of young litter (Liski et al., 1999) which suggests that Q_{10} of the slow and passive pools in CIOM may be lower than that for the structural, metabolic and active pools, i.e., different multiplier functions are required. Four recent studies strengthen the concern about the temperature sensitivity of decay. First, decay rates of forest mineral soil carbon over a global scale gradient are not affected by temperature and CENTURY considerably overestimates turnover times at lower temperatures (Giardina and Ryan, 2000). Second, ecosystem respiration is not related to temperature across a latitudinal gradient of European forests (Valentini et al., 2000). Third, the temperature sensitivity of decay declines with depth in arctic organic soils (Christensen et al., 1999). Fourth, soil respiration did not increase significantly in a Swedish long-term soil warming experiment (Jarvis and Linder, 2000). At the same time, estimates of forest carbon sinks in response to climate warming are critically dependent on the assumed sensitivity of soil organic carbon decay to temperature (Grace and Rayment, 2000). Laboratory incubations over a range of temperatures and decay states are required to confirm that the function chosen here is appropriate for forest floor materials of the western boreal.

As discussed previously, FFC estimates by CIOM showed that climatic zone had little or no effect; in contrast, the field study found a strong effect of climate (Nalder and Wein, 1999). CIOM also predicted much less difference among climatic zones than indicated by the CIDET study (Table 6-10) which raises the question of whether the decay routines are sensitive enough to climate. Such lack of sensitivity could be due to the nitrogen multiplier, temperature multiplier or moisture multipliers being incorrectly estimated. It is unlikely the nitrogen multiplier is at fault, as this has only a small effect on FFC. The temperature multiplier has a large effect (e.g., see Figure 6-7), but the mean values for this do reflect expected zonal differences (Table 6-12). Mean moisture multipliers, however, vary little among zones (Table 6-12). This is surprising because there were considerable differences in a simple *P*-PET climatic moisture index (Hogg, 1994), which ranged from 7 mm in zone 1 to 187 mm in zone 3 (Table 6-1). Since the model is not sensitive to the shape of the multiplier response function (Figure 6-7), it seems likely that the water balance routine is overestimating soil moisture. This is borne out by the validation runs for the SSA-OA site which gave results close to field capacity whereas there were relatively large seasonal variations in observed data (Table 6-8), at least in 1994. Although the water balance routine has given satisfactory results in many CENTURY simulations, it does require application of a PET scaling factor (e.g., Peng et al., 1998, Table 2c) without any rationale for choosing that scalar (Metherell et al., 1994). Nor has the routine previously been specifically validated for boreal forests. Given suitable field data, it may be possible to validate or re-parameterize the routine for the western boreal. Use of monthly timesteps, however, remains problematical because of the episodic nature of rain and the extremely nonlinear processes involved in soil wetting and drying. Improved estimates of soil moisture and decay responses would probably require finer timesteps (e.g., Granier et al., 1999).

It should be noted that the lack of sensitivity of the moisture multiplier function is at least partially due to the high moisture levels calculated by the water balance. It is believed that the moisture multiplier function is a reasonable approximation, but its shape has not been validated against laboratory data because appropriate data do not exist. There is a need, therefore, for laboratory decomposition studies using forest floor substrates from upland forests of the western boreal to test the effect of moisture. It should also be noted that CIOM is based on the same assumption as CENTURY (Parton et al., 1987; Parton et al., 1993) that temperature and moisture act independently, but this is a poor assumption: many data show that the shape of the temperature response function varies with moisture and vice versa (e.g., see Flanagan and Veum, 1974; Bunnell et al., 1977; Boddy, 1983; Schlentner and van Cleve, 1984; Taylor and Parkinson, 1988; Bowden et al., 1998; Chen et al., 2000a). It is important, therefore, that the suggested laboratory studies also assess interactive effects with temperature

Conclusions

The forest floor in upland stands of the western boreal forest is a large component of the C budget in these stands and acts as an important control on many key processes (Chapter 1). Yet its dynamics are poorly known. This thesis represents the first extensive study of boreal forest floor dynamics. Field studies with six chronosequences have shown that the observed dynamics make forest floor C storage sensitive to climate change (Nalder and Wein, 1999). It may, therefore, represent a significant feedback on climate change. Quantification of such long-term feedbacks can only be addressed through modelling, but there are substantial difficulties to be overcome. Not the least of these is developing a model that will accurately simulate tree dynamics (as illustrated by Chapter 5) although approaches at high temporal resolution are promising (e.g., Grant and Nalder, 2000). The input-output model developed here explains some of the observed dynamics, and more importantly has highlighted the uncertainties in simulating forest floor dynamics. Some uncertainties derive from the semi-empirical nature of the model, and may be resolved with a more complex, process-based approach. There are, however, still formidable obstacles in parameterizing and validating such a model due to lack of data. Laboratory studies are required to confirm appropriate decay rate parameters as well as the influence of temperature and moisture on these decay rates. At the same time, field studies are urgently needed to obtain more reliable litter data, particularly fine root turnover, foliage retention time for *P. banksiana*, snag and log dynamics, and annual mortality for moss and lichen. As a lower priority, the controls on shrub species and growth need to be elucidated as well as the controls on lichen development in *P. banksiana* stands. Finally, nitrogen budgets need to be developed for stands in the western boreal so that potential N limitations on growth and decay can be properly assessed; the largest uncertainty surrounds N fixation.

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Tables

Table 6-1. Characteristics of the six chronosequences. Means are shown with standard deviations. NA, not applicable.

	P. banksiana			*P tremuloides*		
	Zone 1	Zone 2	Zone 3	Zone 1	Zone 2	Zone 3
Number of stands	14	10	12	17	17	11
Minimum and maximum age, years	16-111	16-135	30-82	36-132	14-149	28-112
Species dominance, %	99±3	100±1	93±6	93±8	93±10	98±3
Mean annual temperature, °C	-0.7±0.2	-3.2±0.3	-3.9±0.5	-0.2±0.4	-3.0±0.3	-3.3±0.5
Annual precipitation, mm	491±17	387±18	508±21	471±19	385±20	503±14
Climate moisture index[a], mm	43±43	49±28	187±15	7±36	39±30	153±23
Mineral soil						
Bulk density, Mg m^{-3}	1.39±0.06	1.29±0.10	1.33±0.08	1.27±0.18	1.09±0.21	0.97±0.07
Available water holding capacity, g g^{-1}	6%±2%	7%±4%	7%±4%	14%±6%	13%±5%	16%±3%
Number of stands in each texture class[b]	14-0-0-0	10-0-0-0	12-0-0-0	1-10-4-2	5-10-1-1	0-0-1-10
Shrubs, gC m^{-2}	28±32	41±65	38±49	114±120	89±57	301±280
Moss dominance, %	50±45	73±39	35±27	NA	NA	NA
Forest floor, kgC m^{-2}	1.29±0.47	1.52±0.49	1.17±0.27	3.09±0.53	2.93±1.16	2.26±0.47

[a] Climatic moisture index is calculated as annual precipitation minus potential evaporation (Hogg, 1994)

[b] Texture classes are coarse, medium, moderately fine, and fine as described in Nalder and Wein (1999).

Table 6-2. Models, coefficients and fits from a general linear regression of chronosequence vegetation characteristics as a function of stand age and other significant site variables. Number of stands is 80. PIBA, *P. banksiana*; POTR, *P. tremuloides*; age, stand age; spp, species; mat, mean annual temperature (°C); sat, percent saturation (volumetric water holding capacity) of upper layer of mineral soil; wp, percent wilting point (volumetric water holding capacity) of upper layer of mineral soil;

	1st Term	2nd Term	3rd Term	4th Term	R^2
Tree Foliage C (kgC m^{-2})					
Model	ln(age+1)*spp	ln(age+1)*mat			0.96
Term significance	< 0.001	0.02			
PIBA coefficients	4.26E-2	1.25E-3			
POTR coefficients	2.80E-2	1.25E-3			
Tree Branch C (kgC m^{-2})					
Model	ln(age+1)	age*spp	age*mat*spp	age*sat*spp	0.95
Term significance	< 0.001	< 0.001	0.001	0.003	
PIBA coefficients	9.30E-2	4.03E-3	7.281E-5	-4.93E-5	
POTR coefficients	9.30E-2	1.11E-2	8.148E-4	-9.87E-5	
Tree Stem C (kgC m^{-2})					
Model	age*spp	age*mat*spp	age^2*sat*spp		0.94
Term significance	< 0.001	< 0.001	0.03		
PIBA coefficients	6.64E-2	6.60E-3	-6.65E-7		
POTR coefficients	1.07E-1	9.49E-3	-4.21E-6		
Log(Tree Stem Density (stems ha^{-1}))					
Model	Intercept	log(age)	mat		0.66
Term significance	< 0.001	< 0.001	< 0.001		
Coefficients	5.708	-1.265	6.47E-3		
Canopy height (m)					
Model	age*spp	age^2*spp	age*mat*spp		0.99
Term significance	< 0.001	< 0.001	< 0.001		
PIBA coefficients	0.286	-7.52E-4	1.33E-2		
POTR coefficients	0.441	-1.66E-3	1.88E-2		
Shrub wood C (kgC m^{-2})					
Model	age*spp	age*mat*wp			0.66
Term significance	< 0.001	< 0.001			
PIBA coefficients	-2.82E-5	-1.06E-5			
POTR coefficients	4.71E-4	-1.06E-5			
Shrub foliage C (kgC m^{-2})					
Model	age*spp	age*mat*wp			0.70
Term significance	< 0.001	< 0.001			
PIBA coefficients	-1.02E-6	-1.94E-6			
POTR coefficients	4.71E-4	-1.94E-6			
Moss-plus-lichen C (kgC m^{-2})					
Model	age*sat*spp				0.87
Term significance	< 0.001				
PIBA coefficients	5.49E-5				
POTR coefficients	0.0				

Table 6-3. Temporal distribution of total surface and root litter over each year as used in GROWTH submodel.

Month	*P. banksiana*		*P. tremuloides*	
	Surface litter	Root litter	Surface litter	Root litter
Jan	4%	0%	4%	0%
Feb	4%	0%	4%	0%
Mar	4%	0%	4%	0%
Apr	5%	1%	4%	1%
May	7%	6%	4%	6%
Jun	8%	15%	4%	15%
Jul	5%	30%	4%	30%
Aug	10%	30%	4%	30%
Sep	35%	15%	56%	15%
Oct	8%	3%	4%	3%
Nov	6%	0%	4%	0%
Dec	4%	0%	4%	0%

Table 6-4. C:N ratios and lignin fractions of each vegetation and litter component used in GROWTH submodel.

Vegetation component	*P. banksiana*		*P. tremuloides*		Source (numbers refer to footnotes)
	C:N	Lignin fr.	C:N	Lignin fr.	
Tree foliage	55		20		1, 2
Tree Stem	534		357		3
Tree Branch	534		357		3
Tree Stump	534		357		3
Tree Coarse Roots	123.5		98.8		Assumed same as litter
Tree Fine Roots	60.5		48.4		Assumed same as litter
Shrub foliage	26		26		Assumed 60% of that for litter
Shrub wood	100		100		Estimate
Moss-plus-lichen	58		58		4
Tree foliage litter	39	0.328	70	0.144	5
Tree Stem litter	534	0.283	357	0.2	3
Tree Branch litter	534	0.283	357	0.2	3
Tree Stump litter	534	0.283	357	0.2	3
Tree Coarse Root litter	123.5	0.225	98.8	0.203	6
Tree Fine Root litter	60.5	0.36	48.4	0.324	As above
Shrub foliage litter	44	0.246	44	0.246	7
Shrub wood litter	100	0.25	100	0.25	Estimate
Moss-plus-lichen litter	53.5	0.241	53.5	0.241	7

[1] (Vogel and Gower, 1998)
[2] (Peterson and Peterson, 1992)
[3] (Alban and Pastor, 1993)
[4] (Weber and Van Cleve, 1981)
[5] (Trofymow et al., 1995)
[6] (Taylor et al., 1991)
[7] (Fyles and McGill., 1987)

Table 6-5. Sensitivity of total forest floor C (TFFC) to differing assumptions.

Orignal assumption	Modified assumption	Change in TFFC	
		P. banksiana	*P. tremuloides*
Annual litter distributed over months as per Table 6-3	Annual litter evenly distributed over months	-1.1%	-1.2%
Min. monthly PET=1 mm	Min. monthly PET=0 mm	-1.5%	-0.3%
N multiplier defined by Michaelis-Menten function	N multiplier =1.0	-4.4%	-0.1%
No extra soil N after fire	5 g N m^{-2} added to soil in year after fire	-0.2%	0.0%
Snag breakdown defined by Weibull function	Snag breakdown defined by exponential function	+0.9%	+1.3%
Vertical distribution of coarse root biomass is same as for fine roots	Fixed vertical distribution of coarse root biomass (25% to forest floor, 50% to upper 20 cm of mineral soil)	+0.7%	-4.7%
Branch litter only from self-pruning	Branch litter equal to that from self-pruning + 50%	+3.7%	+4.5%

Table 6-6. Simulated aboveground litterfall (gC m^{-2} yr^{-1}) compared with observed data for BOREAS intensive study areas and other sites in the western boreal. These data do not include bole and branch litter. Where applicable, biomass values have been converted to C density assuming 50% C content. SSA, Southern Study Area; NSA, Northern Study area; OA, Old Aspen site; OJP, Old Jack Pine site.

Site/region	Years	Litterfall (gC m^{-2} yr^{-1})
Simulated *P. tremuloides*		
SSA-OA	-	125
NSA-OA	-	107
Observed *P. tremuloides*		
SSA-OA[1]	1993, 1994	123-124
NSA-OA[1]	1993, 1994	74-102
Alberta – Kannanaskis[2]	1968, 1969, 1970	97-123
Simulated *P. banksiana*		
SSA-OJP	-	48
NSA-OJP	-	41
Observed *P. banksiana*		
SSA-OJP[1]	1993, 1994	51-52
NSA-OJP[1]	1993, 1994	24-36
Alberta - Slave Lake[3]	1983	60-172
Alberta - Fort MacKay[3]	1983	21-51
SSA[4]	1994	49-71
NSA[4]	1994	34-62

[1] Data from Table 6 of Gower et al. (1997) for each of 2 years

[2] Data from Table 2 of Cragg et al. (1977) for each of 3 years at a single site

[3] Data from Table 2 of Fyles et al. (1986) for 8 different stands over 1 year

[4] Data from Table 4 of Vogel & Gower (1998) for stands with and without alder understorey

Table 6-7. Comparison of simulated soil respiration with various observed data. Simulated data represent microbial respiration for the BOREAS Southern Study area (SSA) old aspen (OA) and old jack pine (OJP) sites, and are the means of 10 years. Observed data are for the periods reported, or else approximated means for 7 days from cited figures, and have been converted to common units (gC m^{-2} day^{-1}).

Site	Source of Respiration	Seasonal Minimum		Seasonal Maximum		Foot-note
		gC m^{-2} d^{-1}	Period	gC m^{-2} d^{-1}	Period	
Simulated SSA-OA	Microbial	0.38	Winter	1.16	Jul	
Simulated SSA-OJP	Microbial	0.25	Winter	0.93	Jul	
1994 SSA-OA	Total soil	0.73	mid-Apr	9.02	mid-Jul	1
1994 SSA-OJP Undisturbed	Total soil	1.45	end-May	4.25	end-Jul	2
1994 SSA-OJP Clear-cut	Total soil	0.52	mid-Sep	1.66	end-Jul	2
Ontario aspen	Total soil	0.60	Apr	1.80	Aug	3
Ontario pine	Total soil	0.95	Nov	1.47	Sep	4
Interior Alaska aspen	Total soil	1.05	early-Apr	4.00	early-Jun	5
As above	Total soil	1.18	early-Apr	3.80	early-Jul	6
Finland Scots Pine	Total soil	0.15	Dec-Feb	1.09	Jun-Aug	7
Finland mixed	Microbial	0.25	May	1.20	August	8
Finland mixed	Root	0.87	May	2.23	August	8
Sweden mixed	Total soil	1.76	May	7.83	August	9

[1] Data from Black et al. (1996, Figure 10).

[2] Data from Striegl and Wickland (1998, Figure 5). Clear-cut site was harvested the previous winter.

[3] Data from Weber (1990, Figure 1) for 1986 for immature *P. tremuloides*.

[4] Data from Weber (1988, Figure 5) for 1983 for mature *P. banksiana*.

[5] Data from Schlentner and van Cleve (1984, Figure 1) for 1980 for mature *P. tremuloides*.

[6] Data from Schlentner and van Cleve (1984, Figure 2) for 1981 for mature *P. tremuloides*.

[7] Data from Pajari (1995, Figure 5) for immature *Pinus sylvestris*.

[8] Data from Pietikainen et al. (1999, Table 4) and are the means of 3 sites across a *Pinus sylvestris-Picea abies* gradient.

[9] Data from Morén and Lindroth (2000) for mature *Picea abies-Pinus sylvestris*.

Table 6-8. Simulated and measured soil temperature and moisture for BOREAS Southern Study Area Old Aspen (SSA-OA) site in 1994. Simulated values are the mean of 20 runs with stochastic climate based on 1951-1981 Normals and represent values at the midpoint of the forest floor and 10 cm depth in mineral soil. SSA-OA measured values are monthly averages taken from data in Figure 1 of Russell and Voroney (1998) for the growing season of 1994 for the humus layer and at 10 cm and 15 cm into the mineral soil for temperature and moisture, respectively. VWC, volumetric water content.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Forest floor T (°C)												
Simulated	-2.5	-2.3	-1.5	1.1	7.4	11.5	14.3	13.4	8.2	4.4	0.7	-0.7
SSA-OA 1994				1.0	6.0	11.0	13.0	14.0	11.0			
Mineral soil T (°C)												
Simulated	0.4	-0.1	0.0	1.6	6.0	8.5	12.2	11.8	8.2	4.7	2.7	1.5
SSA-OA 1994				1.0	5.5	10.0	12.0	13.5	10.7			
Forest floor VWC												
Simulated	18%	18%	18%	19%	17%	16%	16%	17%	18%	18%	18%	18%
SSA-OA 1994				25%	23%	18%	21%	9%	8%			
Mineral soil VWC												
Simulated	19%	19%	19%	19%	17%	17%	16%	17%	18%	19%	19%	19%
SSA-OA 1994				21%	35%	30%	28%	15%	10%			

Table 6-9. Simulated transpiration or evapotranspiration estimates compared with observed data from selected BOREAS sites in 1994. Simulated values are the mean of 20 runs with stochastic climate based on 1951-1981 Normals. Observed data for Southern Study Area Old Aspen site (SSA-OA) are from Figure 1 of Hogg et al. (1997), for Southern Study Area Old Jack Pine site (SSA-OJP) are from Figure 8 of Saugier et al. (1997) and for Northern Study Area Young Jack Pine site (NSA-YJP) are from Figures 2 and 3 of Joiner et al. (1999).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
SSA-OA transpiration (cm)												
Simulated	0.0	0.0	0.0	0.0	4.2	5.4	6.5	5.2	2.4	0.0	0.0	0.0
Observed						7.2	8.3	6.4	3.0			
SSA-OJP transpiration (cm)												
Simulated	0.0	0.0	0.0	0.0	2.0	2.7	3.3	2.6	1.2	0.4	0.0	0.0
Observed					2.0	3.5	3.7	2.9				
NSA-YJP evapotranspiration (cm)												
Simulated	0.1	0.1	0.1	0.3	2.6	3.8	5.4	3.9	1.6	0.5	0.1	0.1
Observed						4.5	4.7	3.3				

Table 6-10. Simulated litter bag decay expressed as percent mass remaining after 3 years compared with regression model predictions from Canadian Intersite Decomposition Experiment (CIDET) (Moore et al., 1999, Table 3) and a decomposition study undertaken in Kananaskis, Alberta (Taylor et al., 1991, Figure 2.b.). Simulations are based on 100 gC m^{-2} of foliage litter of the species being simulated and typical stand conditions in each of four climatic zones, with climatic data for zones 1, 2, 3 and 4 taken from 1951-1980 Normals for Prince Albert, Fort Smith, Thompson and Kananaskis, respectively. Results are the means of runs for stand ages of 10, 20, 30, 40 and 50 years.

Zone	Species	*T* (°C)	*P* (mm)	*L/N*	Simulated	CIDET [1]	Kananaskis [2]
1	*P. banksiana*	0.12	398	25.6	57%	63%	
2	*P. banksiana*	-3.23	349	25.6	59%	69%	
3	*P. banksiana*	-3.94	542	25.6	59%	68%	
4	*P. banksiana*	2.81	657	25.6	57%	55%	55%
1	*P. tremuloides*	0.12	398	20.1	44%	61%	
2	*P. tremuloides*	-3.23	349	20.1	47%	67%	
3	*P. tremuloides*	-3.94	542	20.1	46%	66%	
4	*P. tremuloides*	2.81	657	20.1	43%	53%	49%

[1] Model is Mass=59.44 - 1.63**T* - 0.015**P* + 0.392**L/N*, where Mass, percent mass remaining after 3 years, *T*, Mean Annual Temperature (°C), *P*, Mean Annual Precipitation (mm), and *L/N*, lignin:nitrogen ratio.

[2] Model is Mass=28.0 - 1.1**L/N* + 1.06 if *L/N*<50 otherwise Mass=17

Table 6-11. Simulated annual mean stocks and annual flows of soil mineral nitrogen for *P. tremuloides* and *P. banksiana* in each of the three zones. Values are averaged over 20 years from a stand age of 50 years. Mineral nitrogen represents total NO_3^- and NH_4^+ in forest floor and top 20 cm of mineral soil. Positive flows indicate inputs to soil mineral nitrogen pool and vice versa.

	P. banksiana			*P. tremuloides*		
	Zone 1	Zone 2	Zone 3	Zone 1	Zone 2	Zone 3
Stocks (gN m^{-2})						
Mineral nitrogen	0.97	0.62	0.54	1.99	1.44	1.11
Flows (gN m^{-2} yr^{-1})						
Mineralization	4.99	4.53	4.31	6.55	5.84	5.86
Atmospheric deposition	0.34	0.32	0.38	0.34	0.32	0.38
Fixation	0.48	0.35	0.67	0.48	0.35	0.67
Leaching	-1.13	-0.73	-0.99	-1.63	-1.18	-1.80
Plant uptake	-3.90	-3.89	-3.86	-4.29	-4.22	-4.22
Volatilization	-0.77	-0.55	-0.50	-1.44	-1.09	-0.89

Table 6-12. Decay rate multipliers for each species and climatic zone. Data are the mean of monthly multiplier values over a 150 year simulation. W_{mult}, moisture multiplier; T_{mult}, temperature multiplier; N_{mult}, soil nitrogen multiplier.

Species	Zone	W_{mult}	T_{mult}	N_{mult}
P. banksiana	1	0.984	0.166	0.917
	2	0.986	0.141	0.844
	3	0.986	0.135	0.828
P. tremuloides	1	0.960	0.163	0.991
	2	0.979	0.138	0.977
	3	0.984	0.132	0.954

Figures

Figure 6-1. Simplified diagram of model developed for this study.

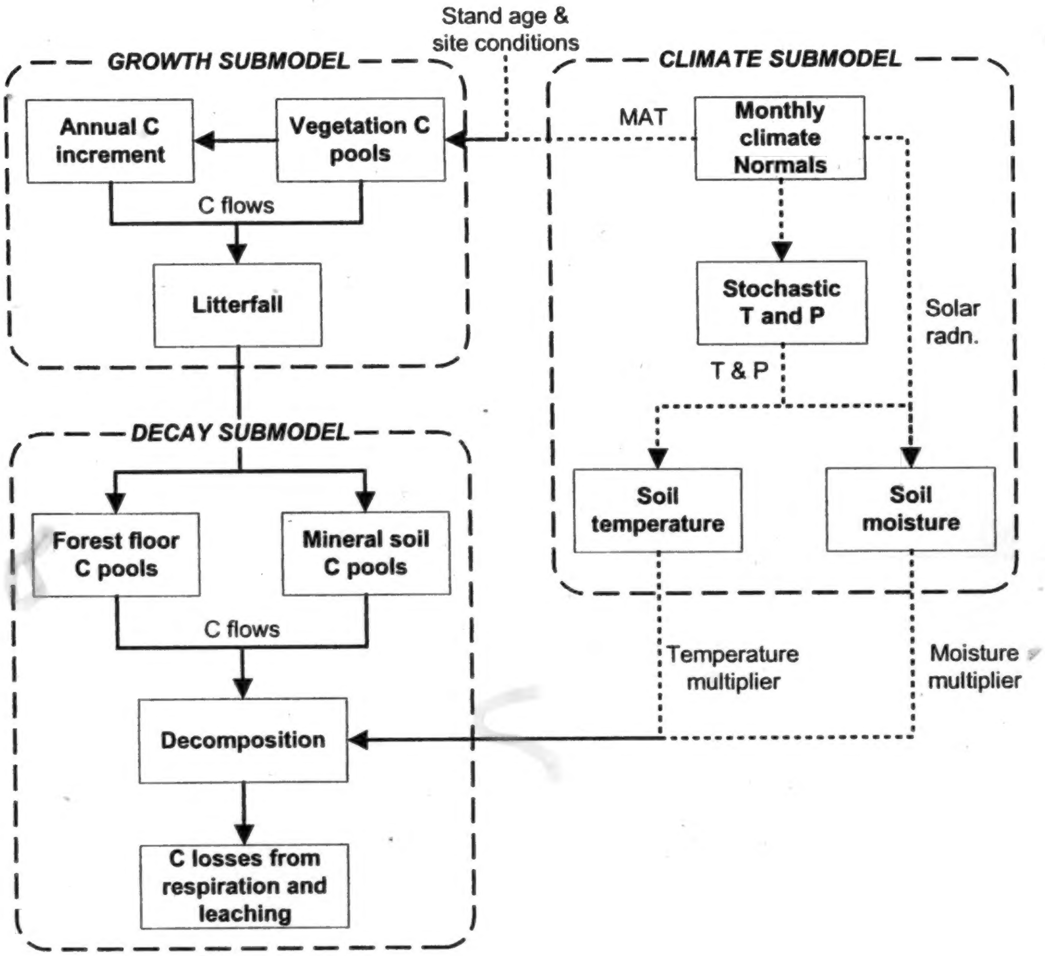

Stand age & site conditions
GROWTH SUBMODEL
Annual C increment
Vegetation C pools
C flows
Litterfall
CLIMATE SUBMODEL
MAT
Monthly climate Normals
Stochastic T and P
Solar radn.
T & P
Soil temperature
Soil moisture
DECAY SUBMODEL
Forest floor C pools
Mineral soil C pools
C flows
Decomposition
C losses from respiration and leaching
Temperature multiplier
Moisture multiplier

Figure 6-2. Western Canada showing location of the three climatic zones in which stands were sampled.

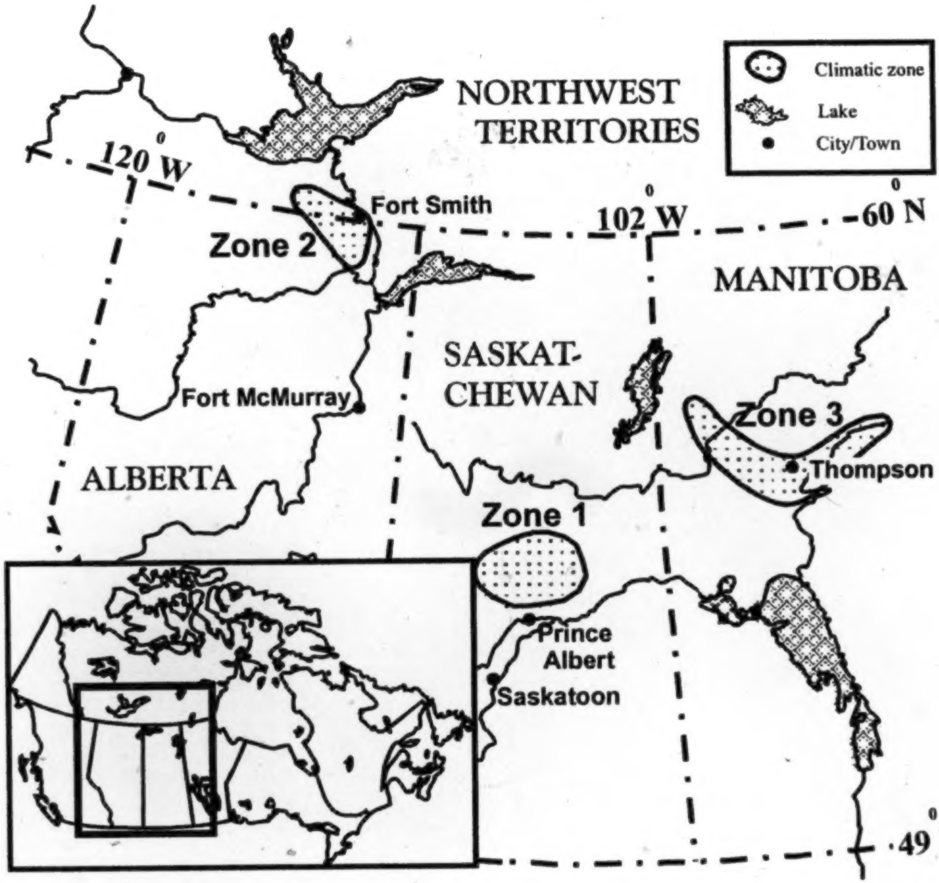

NORTHWEST TERRITORIES
Climatic zone
Lake
City/Town
120° W
102° W
60° N
49° N
Fort Smith
Zone 2
MANITOBA
SASKAT-CHEWAN
Fort McMurray
Zone 3
Thompson
ALBERTA
Zone 1
Prince Albert
Saskatoon

Figure 6-3. Relationship between stand age and six components of vegetation for (a) *P. banksiana* and (b) *P. tremuloides* in study region. Curves have been plotted from regression models in Table 6-2 with mat=0 °C, sat=40% and wp=6%.

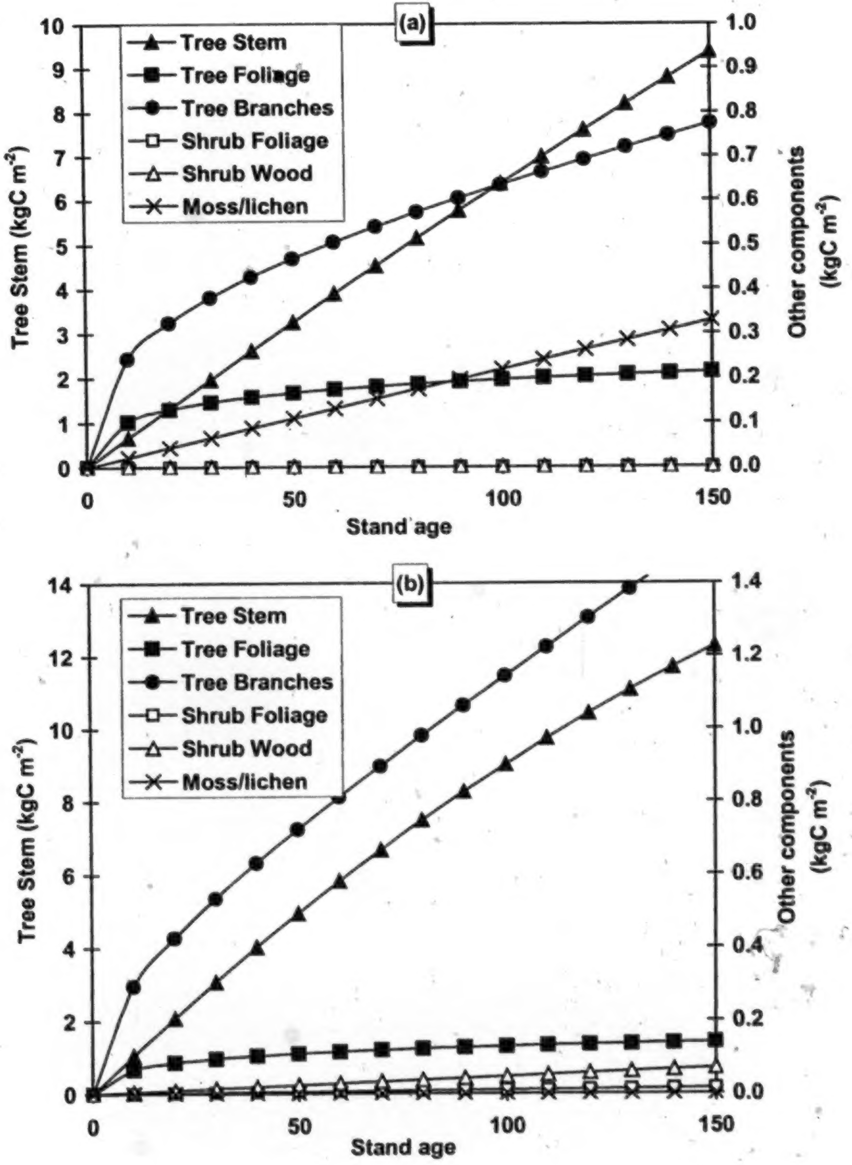


Figure 6-4. Relationship between stem biomass and stump, coarse root and fine root biomass for *P. banksiana* and *P. tremuloides* in boreal forests of western Canada. Fine roots are those below 5 mm in diameter.

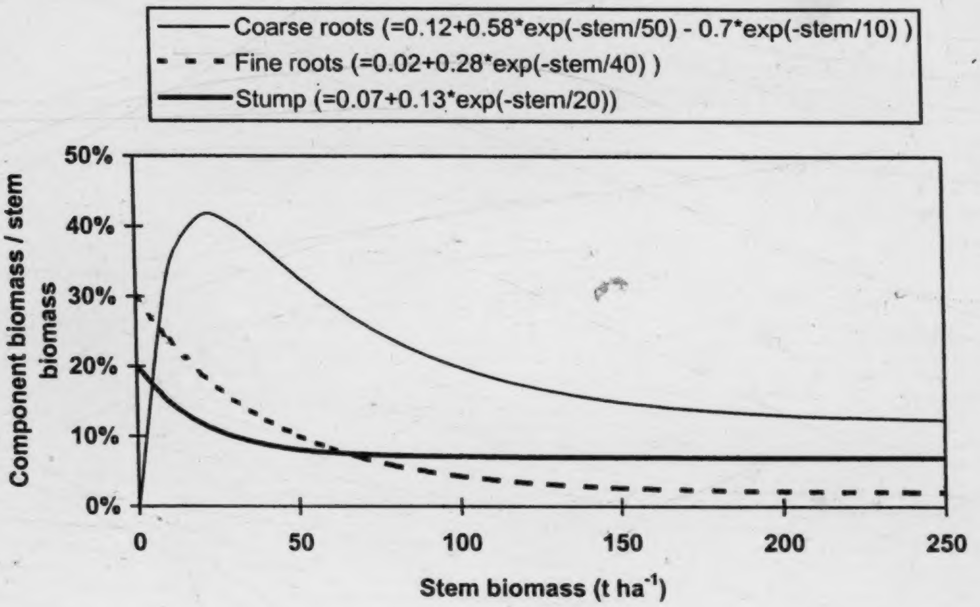


Figure 6-5. Abiotic multiplier functions used in the CLIMATE submodel of CIOM. (a) temperature multiplier, (b) moisture multiplier.

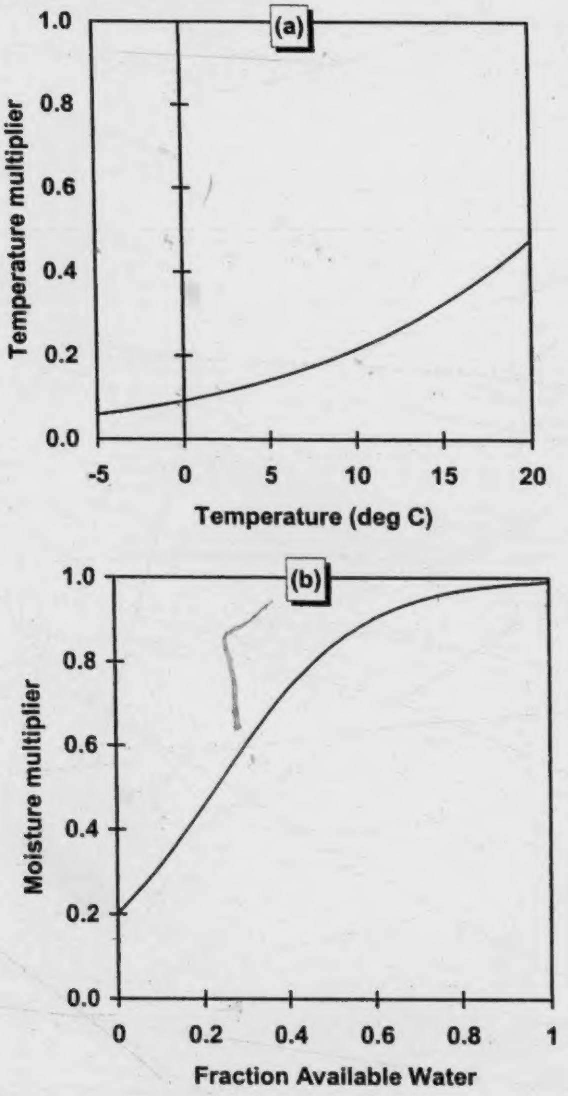


Figure 6-6. Carbon flow diagram for the DECAY submodel. Ovals represent C pools and arrowed lines indicate flow of C. Numbers/symbols beside arrows define the fraction of total flow going from a pool to the indicated destination. Barred arrows indicate loss of C to atmosphere as CO_2. F_m, fraction of litter that is metabolic; T_c, clay content (fraction); T_s, sand content (fraction); W_L, Water leached below 30 cm (cm m^{-1}).

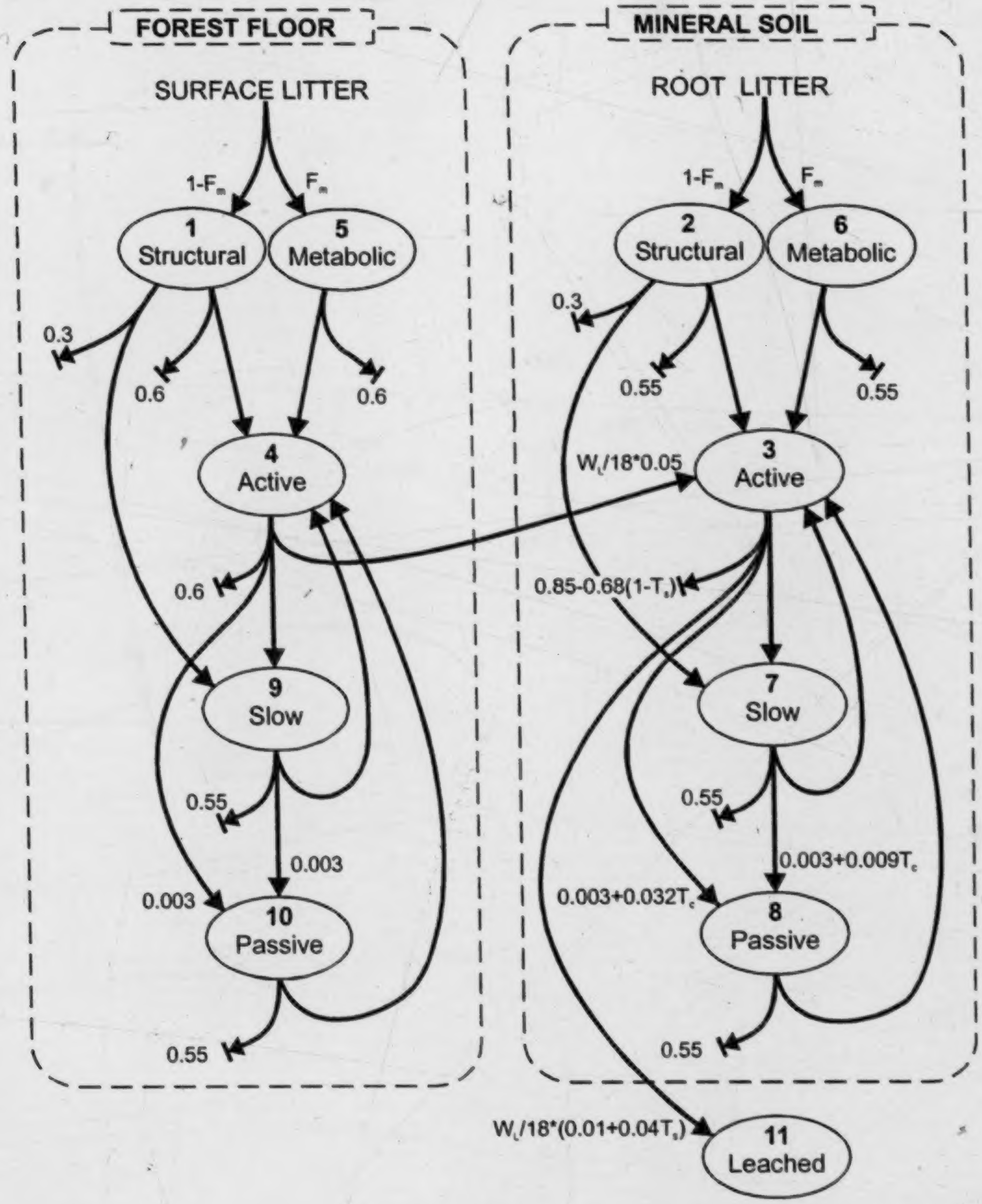

FOREST FLOOR
SURFACE LITTER
1-F_m
F_m
1 Structural
5 Metabolic
0.3
0.6
0.6
4 Active
0.6
9 Slow
0.55
0.003
0.003
10 Passive
0.55
MINERAL SOIL
ROOT LITTER
1-F_m
F_m
2 Structural
6 Metabolic
0.3
0.55
0.55
W_L/18*0.05
3 Active
0.85-0.68(1-T_s)
7 Slow
0.55
0.003+0.009T_c
0.003+0.032T_c
8 Passive
0.55
W_L/18*(0.01+0.04T_s)
11 Leached

Figure 6-7. Sensitivity analysis results. The graphs plot the index of sensitivity (see text) values for *P. tremuloides* against those for *P. banksiana* for 45 parameters and variables, which are indicated by numbered labels as follows: 1, Tree stem growth; 2, Tree branch growth; 3, Tree foliage growth; 4, Tree fine root growth; 5, Shrub foliage growth; 6, Moss-plus-lichen growth; 7, Foliage retention time; 8, Fine root retention time; 9, Shrub wood retention time; 10, Fractional annual moss-plus-lichen mortality; 11, C density of mortally-suppressed trees relative to live trees; 12, Root distribution slope coefficient; 13, Threshold diameter for defining rotten logs; 14, Half-life of snags after stand-replacing fire; 15, Maximum half-life of snags in a living stand; 16, Log half life relative to snag half life; 17, Snag/log decay rate; 18, Fraction of forest floor remaining after fire; 19, Post-fire fraction remaining of tree stems; 20, N fixation slope coefficient; 21, C:N ratio of tree foliage; 22, C:N ratio of tree stems; 23, C:N ratio of tree fine roots; 24, C:N ratio of tree foliage litter; 25, C:N ratio of tree stem litter; 26, C:N ratio of tree fine root litter; 27, Lignin fraction of tree foliage litter; 28, Lignin fraction of tree stem litter; 29, Lignin fraction of tree fine root litter; 30, Potential evapotranspiration; 31, Precipitation adjustment for guage undercatch; 32, Transpiration adjustment for conifers; 33, Forest floor field capacity; 34, Mineral soil field capacity; 35, Temperature multiplier function Arrhenius activation energy; 36, Moisture multiplier function first coefficient; 37, Moisture multiplier function second coefficient; 38, N multiplier function V_{max}; 39, N multiplier function K_m; 40-45, decay constants for carbon pools 1, 4, 5, 9 and 10, respectively.

(See next page for figure)

Figure 6-7. (Continued)

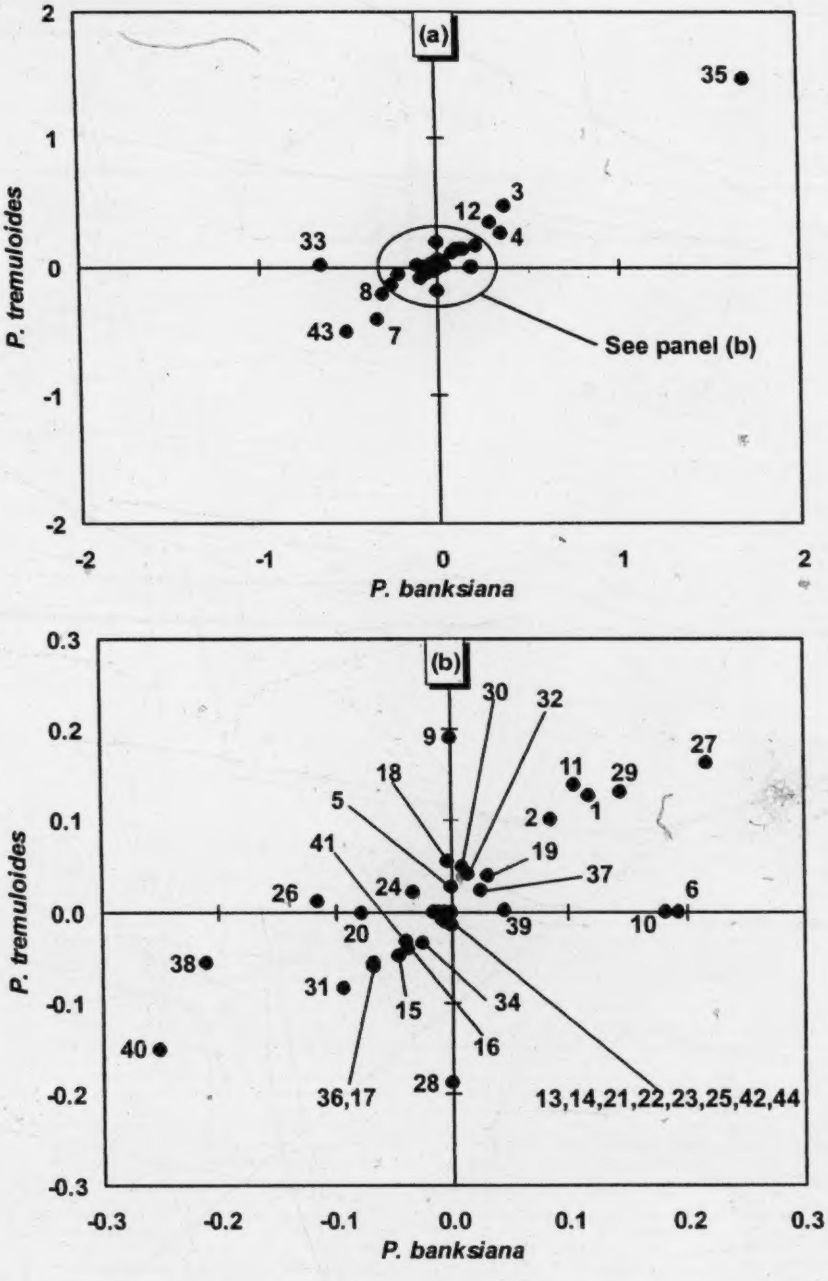


Figure 6-8. Comparison of carbon stocks simulated for each of the BOREAS intensive study sites with observed data from Gower et al. (1997) for aboveground components and Steele et al. (1997) for fine roots (no fine root data are shown for YJP sites). SSA, Southern Study Area; NSA, Northern Study area; OA, Old Aspen site; YJP, Young Jack Pine site; OJP, Old Jack Pine site.

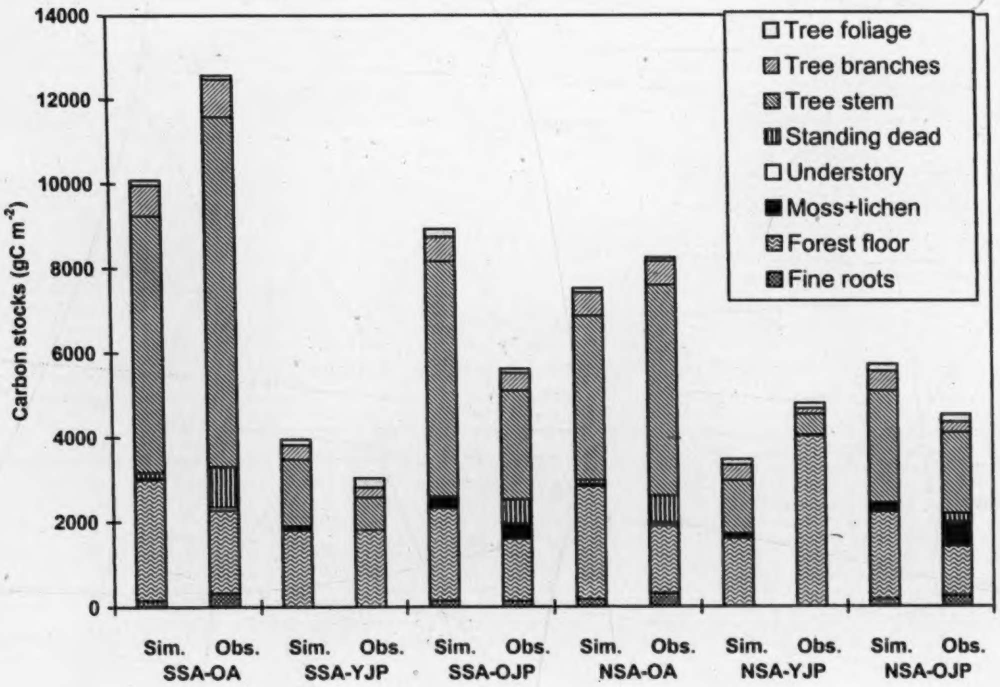
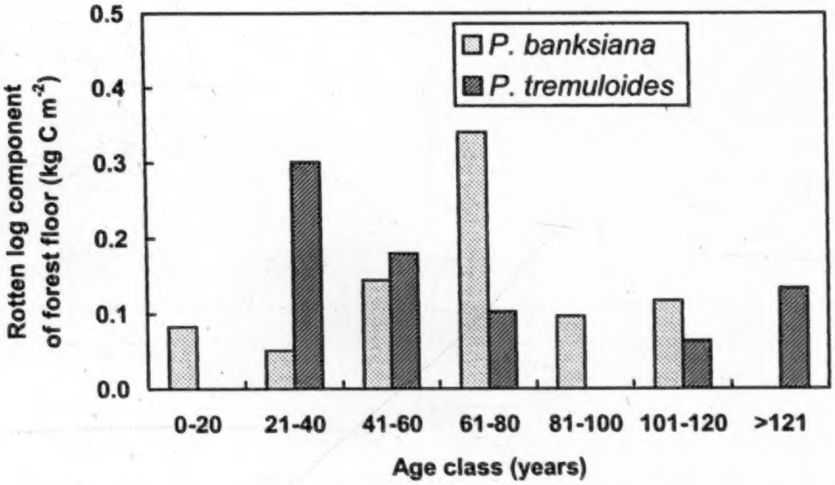


Figure 6-9. Comparison of (a) observed rotten log C dynamics for 80 stands from Figure 5 of Nalder and Wein (1999) compared with (b) simulated data for the same stands. Data have been aggregated into age classes.

(a) Observed



(b) Simulated

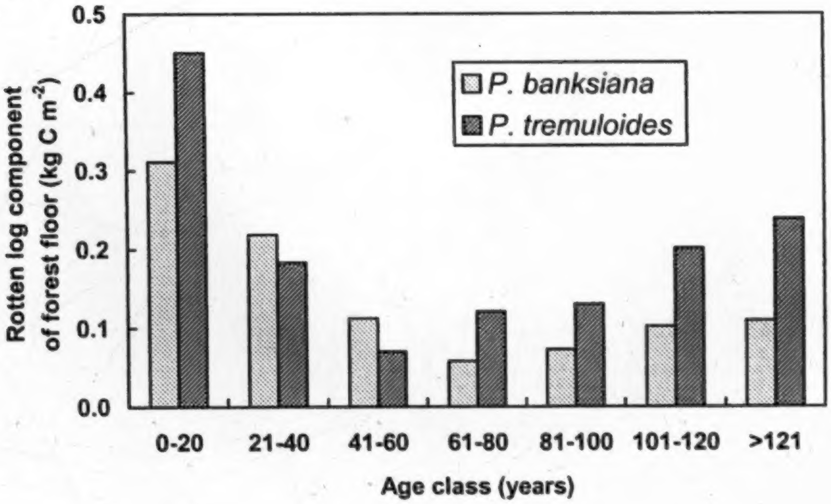


Figure 6-10. Comparison of observed and simulated C:N ratios for a sub-set of the chronosequence stands.

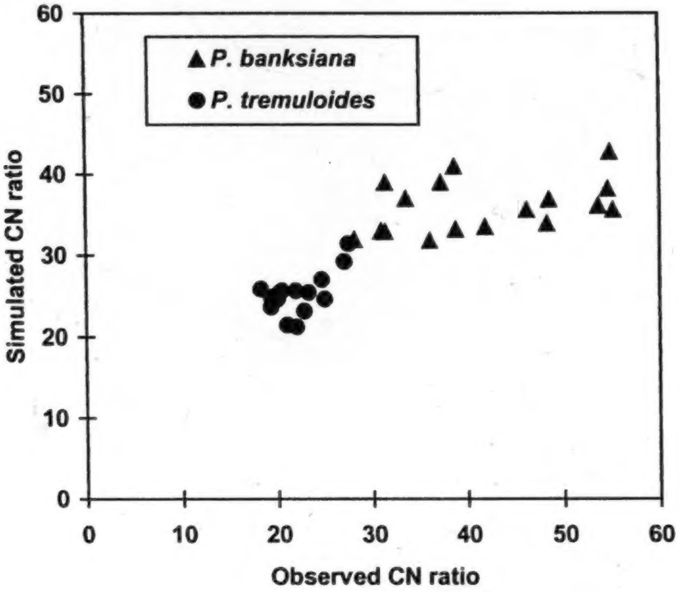


Figure 6-11. Comparison of observed and simulated forest floor carbon (FFC) density for the 80 chronosequnce stands. Closed and open symbols represent simulated and observed data, respectively.

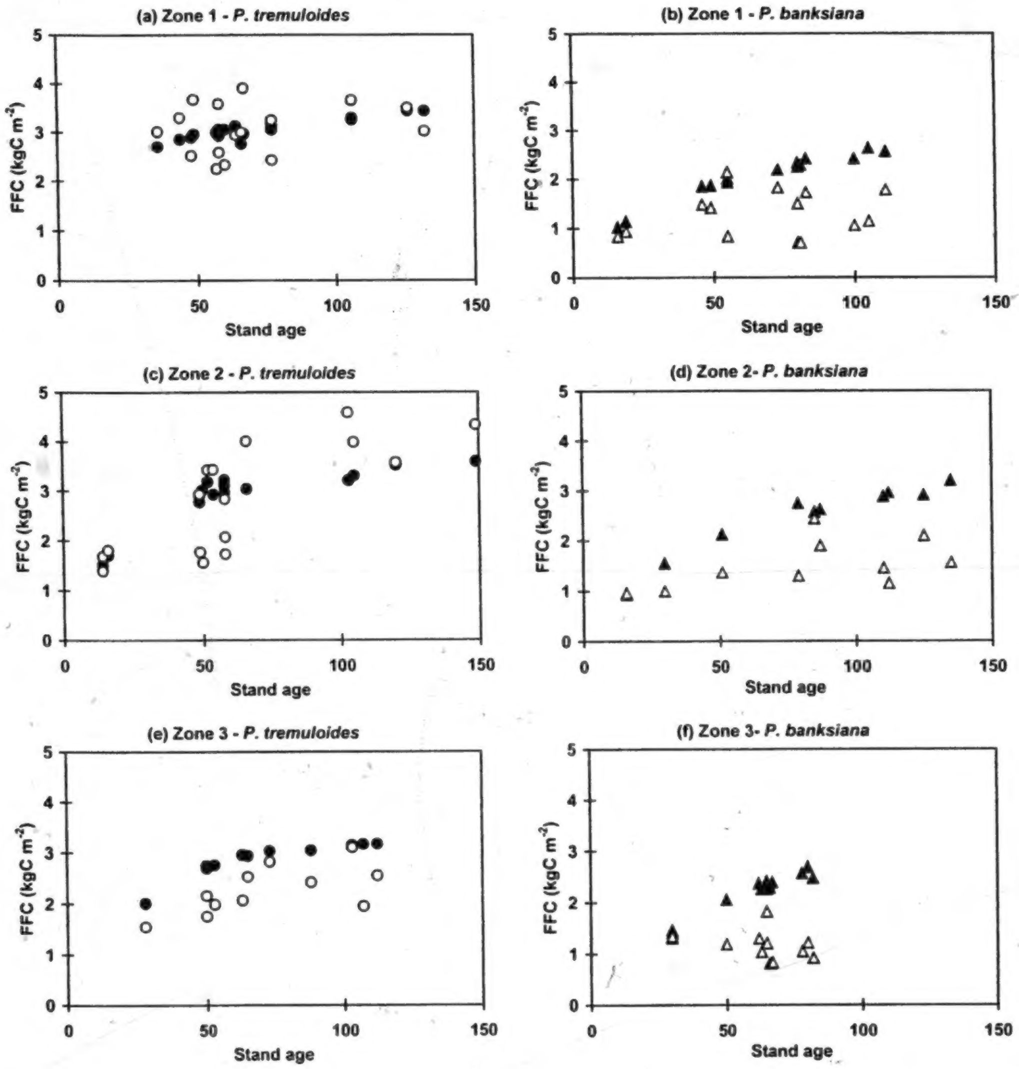


Figure 6-12. Model predictions of (a) FFC and (b) forest floor litter input for *P. banksiana* (open symbols) and *P. tremuloides* (closed symbols) in climatic zones 1, 2 and 3.

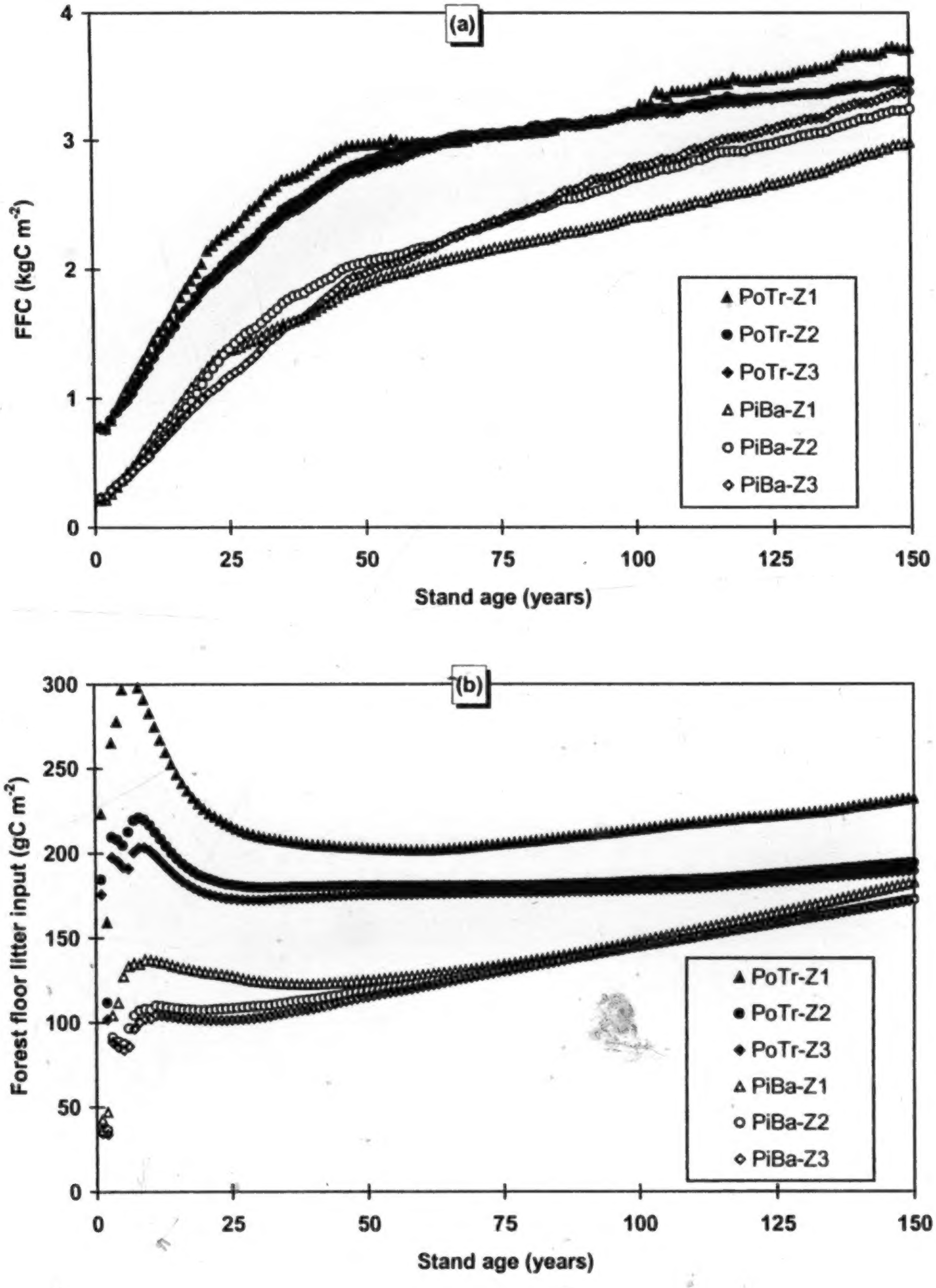
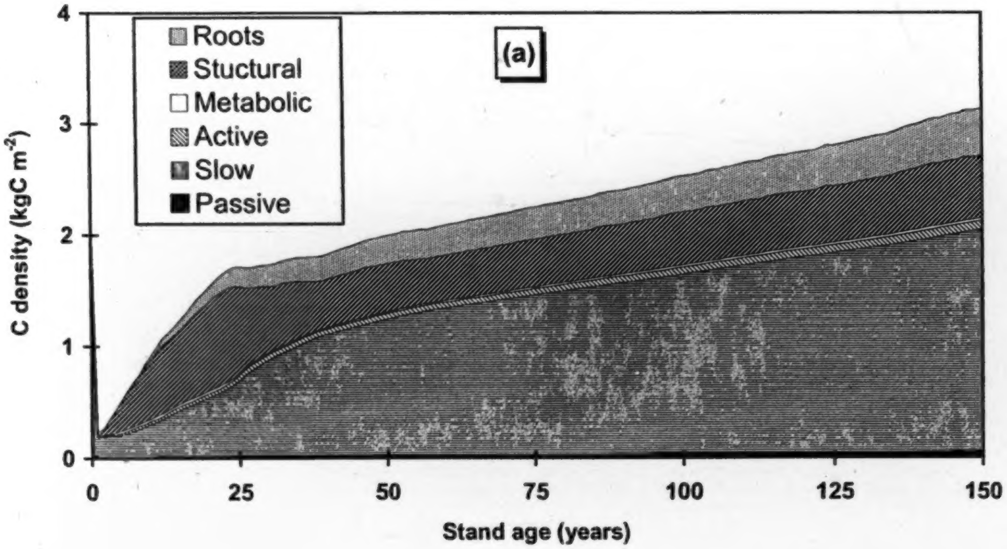


Figure 6-13. Model predictions of forest floor components for (a) *P. banksiana* and (b) *P. tremuloides* in climatic zone 1. The sum of all components is equal to total forest floor carbon (TFFC).



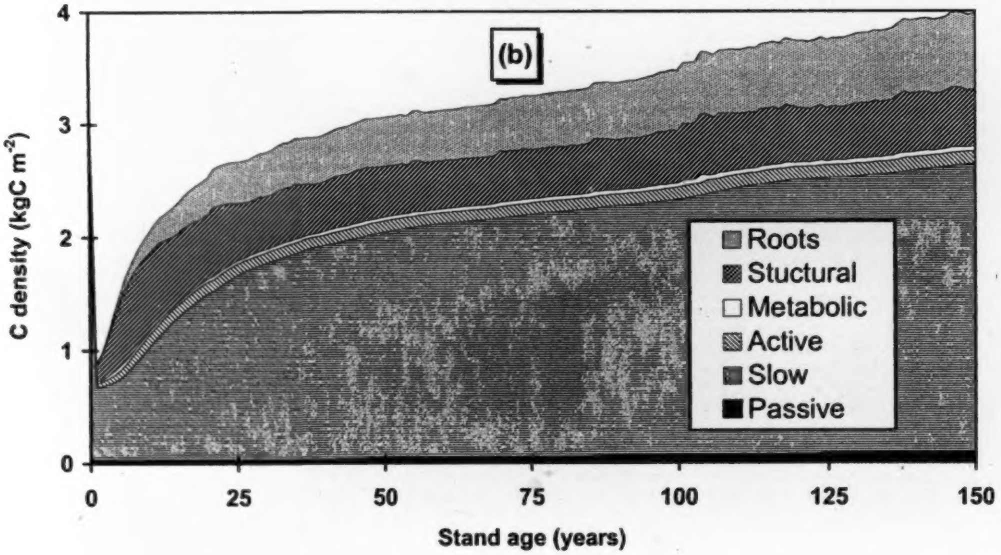


Figure 6-14. Model predictions of each component of forest floor litter input for (a) *P. banksiana* and (b) *P. tremuloides* in climatic zone 1.

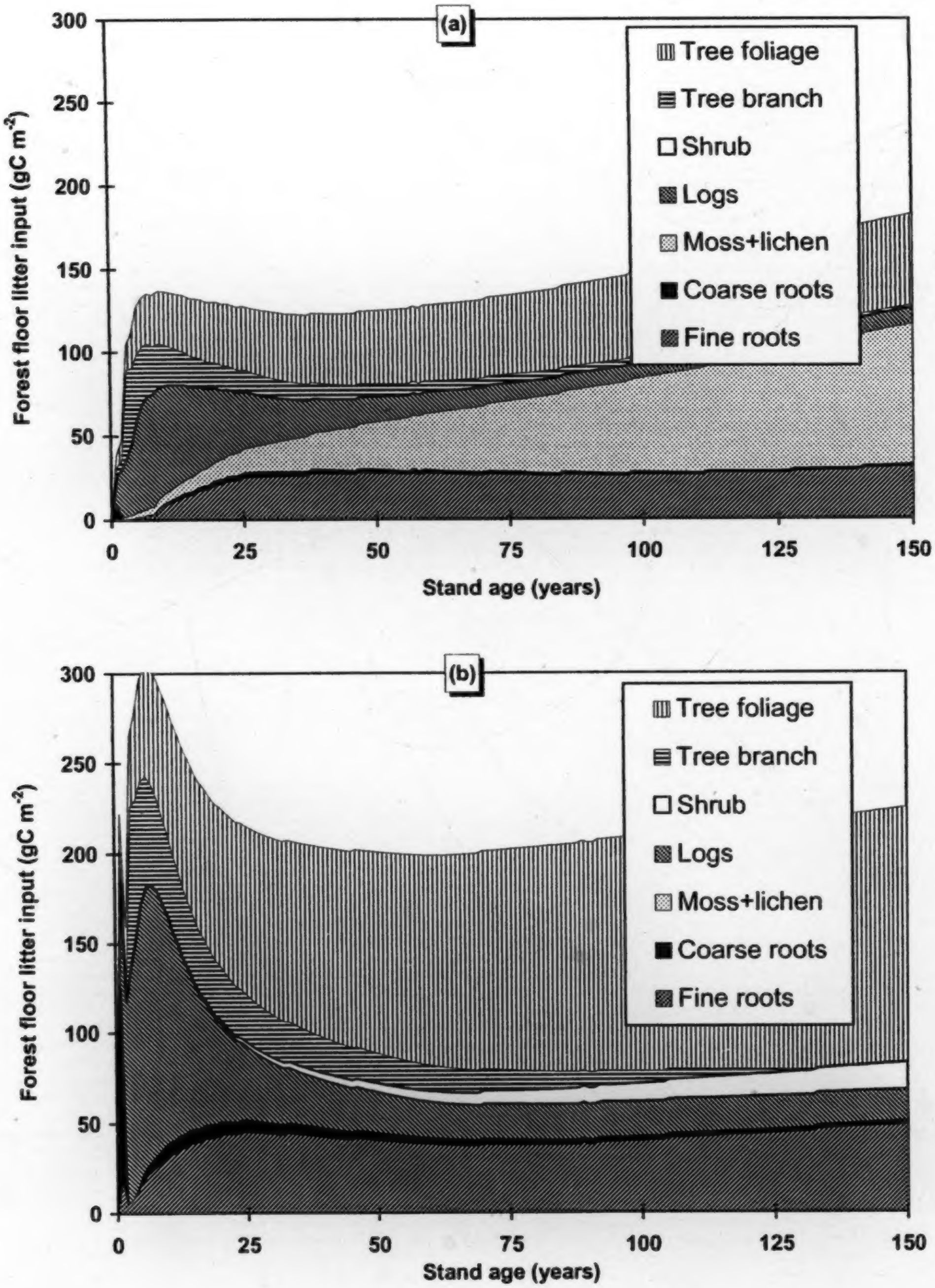


Figure 6-15. CIOM predicted patterns of litter bag mass loss for *P. banksiana* and *P. tremuloides* in climatic zone 1 compared with patterns for *P. sylvestris* and *B. pubescens* in central Sweden. Data for *P. sylvestris* and *B. pubescens* are the means of green and brown leaf mass loss values extracted from Figure 1 of Berg and Ekbohm (1991).

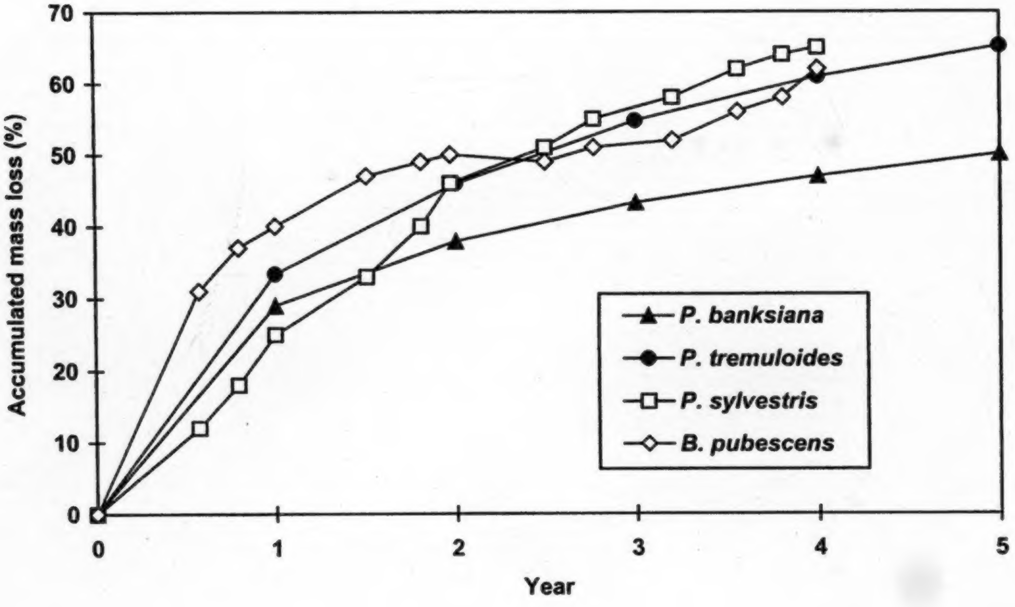
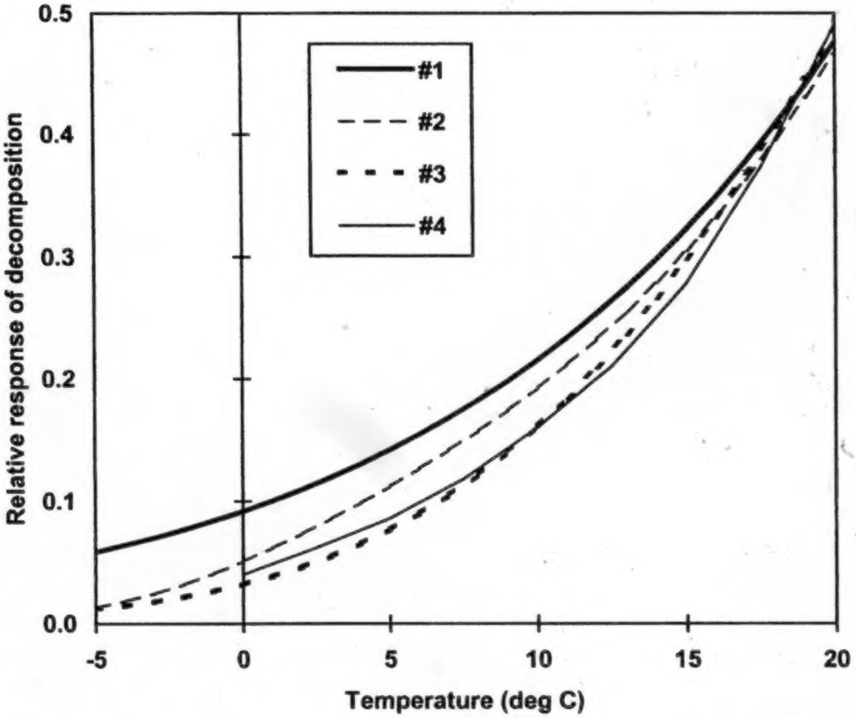


Figure 6-16. Comparison of some functions describing the effect of temperature on decomposition rates. #1, Kätterer et al. (1998, Equation 1); #2, Grant and Rochette (1994, Equation 3); #3, Kirschbaum (1995, Equation 4); #4, Parton et al. (1993, Figure 2).



References

Alban, D.H. and Laidly, P.R., 1982. Generalized biomass equations for jack pine and red pine in the Lake States. Can. J. For. Res., 12: 913-921.

Alban, D.H. and Pastor, J., 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res., 23: 1744-1749.

Alban, D.H., Perala, D.A. and Schaegel, B.E., 1978. Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota. Can. J. For. Res., 8: 290-299.

Alberta Forest Service, 1985. Alberta Phase 3 Forest Inventory: Yield Tables for Unmanaged Stands. Dept. Report 60a. Alberta Energy and Natural Resources, Edmonton, Canada.

Amiro, B.D., Stocks, B.J., Alexander, M.E., Flannigan, M.D. and Wotton, B.M., 2001. Fire, climate change, carbon and fuel management in the Canadian boreal forest. Int. J. Wildland Fire, 10(3-4): 405-413.

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G. and Vinson, T.S., 1993. Boreal forests and tundra. Water, Air, Soil Pollut., 70: 39-53.

Baldocchi, D., Kelliher, F.M., Black, T.A. and Jarvis, P., 2000. Climate and vegetation controls on boreal zone energy exchange. Global Change Biol., 6 Suppl. 1: 69-83.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Man., 133: 13-22.

Berg, B. and Ekbohm, G., 1991. Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. Can. J. Bot., 69: 1449-1456.

Berg, B. and Ekbohm, G., 1993. Decomposing needle litter in lodgepole pine (*Pinus contorta*) and Scots pine (*Pinus sylvestris*) moncultural systems -- is there a maximum mass loss? Scand. J. For. Res., 8: 457-465.

Berg, B., Ekbohm, G., Johansson, M.-B., McClaugherty, C., Rutigliano, G. and Virzo De Santo, A., 1996. Maximum decomposition limits of forest litter types: a synthesis. Can. J. Bot., 74: 659-672.

Berg, B., McClaugherty, C., Virzo De Santo, A., Johansson, M.-B. and Ekbohm, G., 1995. Decomposition of litter and soil organic matter: can we distinguish a mechanism for soil organic matter buildup? Scand. J. For. Res., 10: 108-119.

Berg, B., McClaugherty, C., Virzo De Santo, A. and Johnson, D., 2001. Humus buildup in boreal forests: effects of litter fall and its N concentration. Can. J. For. Sci., 31: 988-998.

Bergeron, Y. and Flannigan, M.D., 1995. Predicting the effects of climate change on fire frequency in the southeastern Canadian boreal forest. Water, Air, Soil Pollut., 82: 437-444.

Black, T.A., denHartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nesic, Z., Lee, X., Chen, S.G., Staebler, R. and Novak, M.D., 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. Global Change Biol., 2: 219-229.

Boddy, L., 1983. Carbon dioxide release from decomposing wood: effect of water content and temperature. Soil Biol. Biochem., 15: 501-510.

Bonan, G.B., 1988. Environmental processes and vegetation patterns in boreal forests. Ph.D. thesis, Department of Environmental Sciences, University of Virginia, Charlotesville, VA. 286 pp.

Bonan, G.B., 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecol. Model., 45: 275-306.

Bonan, G.B., 1990a. Carbon and nitrogen cycling in North American boreal forests I. Litter quality and soil thermal effects in interior Alaska. Biogeochem., 10: 1-28.

Bonan, G.B., 1990b. Carbon and nitrogen cycling in North American boreal forests II. Biogeographic patterns. Can. J. For. Res., 20: 1077-1088.

Bonan, G.B. and Shugart, H.H., 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Syst., 20: 1-28.

Bowden, R.D., Newkirk, K.M. and Rullo, G.M., 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. Soil Biol. Biochem., 30(12): 1591-1597.

Bradshaw, R.H.W. and Zackrisson, O., 1990. A two thousand year history of a northern Swedish boreal forest stand. J. Veg. Sci., 1: 519-528.

Bratley, P., Fox, B.L. and Schrage, L.E., 1983. A Guide to Simulation. Springer-Verlag, New York. 383 pp.

Briggs, D., Smithson, P. and Ball, T., 1989. Fundamentals of Physical Geography. Canadianedition. Copp Clark Pitman Ltd., Mississauga, Ontario, Canada. 594 pp.

Brouzes, R., Lasik, J. and Knowles, R., 1969. The effect of organic amendment, water content and oxygen on the incorporation of $^{15}N_2$ by some agricultural and forest soils. Can. J. Microbiol., 15: 899-905.

Brydges, T.G., 1998. Nitrogen deposition in Canada's Boreal Shield: implications for the Kyoto Protocol. Environ. Pollut., 102 Suppl. 1: 365-370.

Buchmann, N., 2000. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. Soil Biol. Biochem., 32(11-12): 1625-1635.

Bugmann, H., Wullschleger, S.D., Price, D.T., Ogle, K., Clark, D.F. and Solomon, A.M., 2001. Comparing the performance of forest gap models in North America. Clim. Change, 51(3-4): 349-388.

Bunnell, F.L. and Tait, D.E.N., 1974. Mathematical simulation models of decomposition processes. In: Holding, A.J., Heal, O.W., MacLean Jr., S.F. and Flanagan, P.W. (Editors). Soil Organisms and Decomposition in Tundra: Proceedings of the Microbiology, Decomposition, and Invertebrate Working Groups meeting, University of Alaska, Fairbanks Alaska, August 1973, Tundra Biome Steering Committee, Stockholm, Sweden, pp. 207-225.

Bunnell, F.L., Tait, D.E.N., Flanagan, F.W. and van Cleve, K., 1977. Microbial respiration and substrate weight loss. 1. A general model of the influences of abiotic variables. Soil Biol. Biochem., 9: 33-40.

Burton, P.J. and Cumming, S.G., 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water, Air, Soil Pollut., 82: 401-414.

Carroll, S.B. and Bliss, L.C., 1982. Jack pine-lichen woodland on sandy soils in northern Saskatchewan and northeastern Alberta. Can. J. Bot., 60: 2270-2282.

Chapin III, F.S., McGuire, A.D., Randerson, J., Pielke, R., Baldocchi, D., Hobbie, S.E., Roulet, N., Eugster, W., Kasischke, E., Rastetter, E.B., Zimov, S.A. and Running, S.W., 2000. Arctic and boreal ecosystems of western North America as components of the climate system. Global Change Biol., 6 Suppl. 1: 211-223.

Chen, H., Harmon, M.E., Griffiths, R.P. and Hicks, W., 2000a. Effects of temperature and moisture on carbon respired from decomposing woody roots. For. Ecol. Man., 138: 51-64.

Chen, W.J., Chen, J.H. and Cilar, J., 2000b. An integrated terrestrial ecosystem carbon-budget model based on changes in disturbance, climate, and atmospheric chemistry. Ecol. Model., 135(1): 55-79.

Christensen, T.R., Jonasson, S., Callaghan, T.V. and Havstrom, M., 1999. On the potential CO2 release from tundra soils in a changing climate. Applied Soil Ecology, 11(2-3): 127-134.

Clark, J.S., 1988. Effect of climate change on fire regimes in northwestern Minnesota. Nature, 334: 233-234.

Clark, J.S., 1990. Fire and climate change during the last 750 yr in northwestern Minnesota. Ecol. Monogr., 60(2): 135-159.

Cragg, J.B., Carter, A., Leischer, C. and Peterson, E.B., 1977. Litterfall and chemical cycling in an aspen (*Populus tremuloides*) woodland ecosystem in the Canadian Rockies. Pedobiologia, 17: 428-443.

Ecoregions Working Group of Canada, 1989. Ecoclimatic Regions of Canada. Ecol. Land Classif. Ser. 23. Environ. Can. Wildl. Serv., Can. Comm. Ecol. Land Classif., Ottawa, Ontario, Canada.

Environment Canada, 1982. Canadian Climate Normals 1951-1980. Temperature and Precipitation, The North - Y.T. and N.W.T. Atmospheric Environment Service, Environment Canada, Downsview, Ontario, Canada. 56 pp.

Environment Canada, 1983. Canadian Climate Normals 1951-1980. Temperature and Precipitation, Prairie Provinces. Atmospheric Environment Service, Environment Canada, Downsview, Ontario, Canada. 429 pp.

Environment Canada, 1992. The State of Canada's Climate: Temperature change in Canada 1895-1991. State of the Environment Report No. 92-2. Government of Canada, Ottawa, Canada. 36 pp.

Evert, F., 1985. Systems of equations for estimating ovendry mass of 18 Canadian tree species. Inf. Rep. PI-X-59. PNFI, Can. For. Serv., Chalk River, Ontario, Canada.

Finer, L., Messier, C. and De Grandpre, L., 1997. Fine-root dynamics in mixed boreal conifer-broad-leafed forest stands at different successional stages after fire. Can. J. For. Res., 27(3): 304-314.

Flanagan, P.W. and van Cleve, K., 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can. J. For. Res., 13: 795-817.

Flanagan, P.W. and Veum, A.K., 1974. Relationships between respiration, weight loss, temperature and moisture in organic residues on tundra. In: Holding, A.J., Heal, W.O., Maclean Jr., S.F. and Flanagan, P.W., (Editors). Soil Organisms and Decomposition in Tundra. Tundra Biome Steering Committee, Stockholm, pp. 249-277.

Foster, N.W. and Morrison, I.K., 1976. Distribution and cycling of nutrients in a natural *Pinus banksiana* ecosytem. Ecology, 57: 110-120.

Friend, A.D., Shugart, H.H. and Running, S.W., 1993. A physiology-based gap model of forest dynamics. Ecology, 74: 792-797.

Fyles, J.W., LaRoi, G.H. and Ellis, R.A., 1986. Litter production in *Pinus banksiana* dominated stands in northern Alberta. Can. J. For. Res., 16: 772-777.

Fyles, J.W. and McGill., W.B., 1987. Decomposition of boreal forest litters from central Alberta under laboratory conditions. Can. J. For. Res., 17: 109-114.

Giardina, C.P. and Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature, 404: 858-861.

Goldring, D.L. and Stanton, C.R., 1972. Water storage in the forest floor of subalpine forests of Alberta. Can. J. For. Res., 2: 1-6.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J. and Stow, T.K., 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophy. Res., 102(D24): 29029-29041.

Grace, J. and Rayment, M., 2000. Respiration in the balance. Nature, 404: 819-820.

Granier, A., Breda, N., Biron, P. and Villette, S., 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecol. Model., 116(2-3): 269-283.

Grant, R.F., Black, T.A., den-Hartog, G., Berry, J.A., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C. and Nalder, I.A., 1999. Diurnal and annual exchanges of mass and energy between an aspen-hazelnut forest and the atmosphere: Testing the mathematical model Ecosys with data from the BOREAS experiment. J. Geophy. Res. (Atm.), 104(D22): 27699-27717.

Grant, R.F. and Nalder, I.A., 2000. Climate change effects on net carbon exchange of a boreal aspen-hazelnut forest: estimates from the ecosystem model *ecosys*. Global Change Biol., 6: 183-200.

Grant, R.F. and Rochette, P., 1994. Soil microbial respiration at different water potentials and temperatures: theory and mathematical modeling. Soil Sci. Soc. Am. J., 58: 1681-1690.

Grigal, D.F., Brovold, S.L., Nord, W.S. and Ohmann, L.F., 1989. Bulk density of surface soils and peat in the North Central United States. Can. J. Soil Sci., 69: 895-900.

Grigal, D.F. and Ohmann, L.F., 1992. Carbon storage in upland forests of the Lake States. Soil Sci. Soc. Am. J., 56: 935-943.

Hanson, P.J., Edwards, N.T., Garten, C.T. and Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. Biogeochem., 48(1): 115-146.

Hogg, E.H., Black, A., den Hartog, G., Neumann, H.H., Zimmermann, R., Hurdle, P.A., Blanken, P.D., Nesic, Z., Yang, P.C., Staebler, R.M., McDonald, K.C. and Oren, R., 1997. A comparison of sap flow and eddy fluxes of water vapour from a boreal deciduous forest. J. Geophy. Res., 102(D24): 28929-28937.

Hogg, T.H., 1994. Climate and the southern limit of the western Canadian boreal forest. Can. J. For. Res., 24: 1835-1845.

Huang, S., Titus, S.J. and Wiens, D.P., 1992. Comparison of nonlinear height-diameter functions for major Alberta tree species. Can. J. For. Res., 22: 1297-1304.

Huang, W.Z. and Schoenau, J.J., 1997. Seasonal and spatial variations in soil nitrogen and phosphorus supply rates in a boreal aspen forest. Can. J. Soil Sci., 77(4): 597-612.

Ipatov, V.S. and Tarkhova, T.N., 1983. Mutual influence of moss and lichen synusiae in green moss-lichen pine forests. Sov. J. Ecol., 14: 16-21.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. and Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia, 108(3): 389-411.

Jarvis, P. and Linder, S., 2000. Constraints to growth of boreal forests. Nature, (405): 904-905.

Jensen, M.E., Burman, R.D. and Allen, R.G., 1990. Evapotranspiration and irrigation water requirements. Man. Rep. Eng. Pract. No. 70. American Society Civil Engineers, New York, USA.

Johnstone, W.D. and Peterson, E.B., 1980. Above-ground component weights in Alberta *Populus* stands. Inf. Rep. NOR-X-226. Can. For. Serv., North. For. Res. Cent., Edmonton, Alberta.

Joiner, D.W., McCaughey, J.H., Lafleur, P.M. and Bartlett, P.A., 1999. Water and carbon dioxide exchange at a boreal young jack pine forest in the BOREAS northern study area. J. Geophy. Res. (Atm.), 104(D22): 27641-27652.

Karjalainen, T., 1996. The carbon sequestration potential of unmanaged forest stands in Finland under changing climatic conditions. Biomass Bioenergy, 10(5-6): 313-329.

Kattenberg, A., Giorgi, G., Grassl, H., Meehl, G.A., Mitchell, J.F.B., Stougger, R.J., Tokioka, T., Weaver, A.J. and Wigley, T.M.L., 1996. Climate models - projections of future climate. In: Houghton, J.T., Meira Filho, J.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K., (Editors). Climate Change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, UK, pp. 283-357.

Kätterer, T., Reichstein, M., Andrén, O. and Lomander, A., 1998. Temperature dependence of organic matter decomposition: a critical review using literature data analyzed with different models. Biol. Fert. Soils, 27: 258-262.

Kauppi, P.E., Posch, M., Hanninen, P., Henttonen, H.M., Ihalainen, A., Lappalainen, E., Starr, M. and Tamminen, P., 1997. Carbon reservoirs in peatlands and forests in the boreal regions of Finland. Silva Fennica, 31(1): 13-25.

Kauppi, P.E., Tomppo, E. and Ferm, A., 1995. C and N storage in living trees within Finland since 1950's. Plant Soil, 168-169: 633-638.

Kellomäki, S. and Väisänen, H., 1997. Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. Ecol. Model., 97: 121-140.

Kellomäki, S., Väisänen, H. and Strandman, H., 1993. FINNFOR: A model for calculating the response of boreal forest ecosystems to climate change. Res. Note 6. Faculty of Forestry, University of Joensuu, Joensuu, Finland.

Kelly, R.H., Parton, W.J., Crocker, G.B., Grace, P.R., Klir, J., Korschens, M., Poulton, P.R. and Richter, D.D., 1997. Simulating trends in soil organic carbon in long-term experiments using the century model. Geoderma, 81: 75-90.

Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol. Biochem., 27: 753-760.

Klingensmith, K.M. and van Cleve, K., 1993. Denitrification and nitrogen fixation in floodplain successional soils along the Tanana River, interior Alaska. Can. J. For. Res., 23: 956-963.

Kolchugina, T.P. and Vinson, T.S., 1993. Equilibrium analysis of carbon pools and fluxes of forest biomes in the former Soviet Union. Can. J. For. Res., 23: 81-88.

Krankina, O.N. and Harmon, M.E., 1995. Dynamics of the dead wood carbon pool in the Northwestern Russian boreal forests. Water, Air, Soil Pollut., 82: 227-238.

Kurz, W.A., Apps, M.J., Webb, T.M. and McNammee, P.J., 1992. The carbon budget of the Canadian Forest Sector: Phase I. Inf. Rep. NOR-X-326. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta, Canada.

Kurz, W.A., Beukema, S.J. and Apps, M.J., 1996. Estimation of root biomass and dynamics for the carbon budget model of the Canadian forest sector. Can. J. For. Res., 26(11): 1973-1979.

Landhäusser, S.M. and Wein, R.W., 1993. Postfire vegetation recovery and tree establishment at the Arctic treeline: climate-change vegetation response hypotheses. J. Ecol., 81: 665-672.

Larsen, C.P.S., 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeogr., 24: 663-673.

Lee, P., 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Man., 105: 263-272.

Lenihan, J.M. and Neilson, R.P., 1995. Canadian vegetation sensitivity to projected climatic change at three organizational levels. Clim. Change, 30: 27-56.

Li, Z., Apps, M.J., Banfield, E. and Kurz, W.A., 2002. Estimating net primary production of forests in the Canadian Prairie Provinces using an inventory-based carbon budget model. Can. J. For. Sci., 32(1): 161-169.

Linacre, E.T., 1977. A simple formulae for estimating evaporation rates in various climates, using temperature data alone. Agricultural Meterology, 18: 409-424.

Linn, D.M. and Doran, J.W., 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. Soil Sci. Soc. Am. J., 48: 1267-1272.

Liski, J., Ilvesniemi, H., Mäkelä, A. and Starr, M., 1998. Model analysis of the effects of soil age, fires and harvesting on the carbon storage of boreal forest soils. Eur. J. Soil Sci., 49(3): 407-416.

Liski, J., Ilvesniemi, H., Makela, A. and Westman, C.J., 1999. CO_2 emissions from soil in response to climatic warming are overestimated - The decomposition of old soil organic matter is tolerant of temperature. Ambio, 28(2): 171-174.

Liski, J. and Westman, C.J., 1995. Density of organic carbon in soil at coniferous forest sites in southern Finland. Biogeochem., 29: 183-197.

Liski, J. and Westman, C.J., 1997. Carbon storage in forest soil of Finland: 1. Effect of thermocline. Biogeochem., 36: 239-260.

MacLean, D.A. and Wein, R.W., 1977. Nutrient accumulation for postfire jack pine and hardwood succession patterns in New Brunswick. Can. J. For. Res., 7: 562-578.

MacLean, D.A. and Wein, R.W., 1980. Simulation of wildfire effects on the nitrogen cycle of a *Pinus banksiana* ecosystem in New Brunswick. Ecol. Model, 10: 167-192.

Makipaa, R., Karjalainen, T., Pussinen, A. and Kellomaki, S., 1999. Effects of climate change and nitrogen deposition on the carbon sequestration of a forest ecosystem in the boreal zone. Can. J. For. Res., 29(10): 1490-1501.

McGuire, A.D., Melillo, J.M., Kicklighter, D.W. and Joyce, L.A., 1995. Equilibrium responses of soil carbon to climate change: empirical and process based estimates. J. Biogeogr., 22: 785-796.

McKay, D.C. and Morris, R.J., 1985. Solar radiation data analyses for Canada 1967-1976. Atmospheric Environment Service, Environment Canada, Ottawa, Ontario.

Medlyn, B.E., McMurtrie, R.E., Dewar, R.C. and Jeffreys, M.P., 2000. Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration. Can. J. For. Res., 30(6): 873-888.

Metherell, A.K., Harding, L.A., Cole, C.V. and Parton, W.J., 1994. CENTURY soil organic matter model environment, technical documentation, Agroecosystem version 4.0. GPSR Technical Report No. 4. Great Plains System Research Unit, USDA-ARS., Fort Collins, CO.

Moore, T.R., Trofymow, J.A., Taylor, B., Prescott, C., Camiré, C., Duschene, L., Fyles, J., Kozak, L., Kranabetter, M., Morrison, I., Siltanen, M., Smith, S., Titus, B., Visser, S., Wein, R. and Zoltai, S., 1999. Litter decomposition rate in Canadian forests. Global Change Biol., 5: 75-82.

Morén, A.S. and Lindroth, A., 2000. CO_2 exchange at the floor of a boreal forest. Agric. For. Meteorol., 101(1): 1-14.

Nalder, I.A. and Wein, R.W., 1998a. A new forest floor corer for rapid sampling, minimal disturbance and adequate precision. Silva Fennica, 32(4): 373-382.

Nalder, I.A. and Wein, R.W., 1998b. Spatial interpolation of climatic Normals: test of a new method in the Canadian boreal forest. Agric. For. Meteorol., 92(4): 211-225.

Nalder, I.A. and Wein, R.W., 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochem. Cycles, 13(4): 951-968.

Nalder, I.A., Wein, R.W., Alexander, M.E. and de Groot, W.J., 1999. Physical properties of dead and downed round-wood fuels in the boreal forests of western and northern Canada. Int. J. Wildland Fire, 9(2): 85-99.

Ojima, D.S., Parton, W.J., Schimel, D.S., Scurlock, J.M.O. and Kittel, T.G.F., 1993. Modeling the effects of climatic and CO-2 changes on grassland storage of soil C. Water, Air, Soil Pollut., 70(1-4): 643-657.

Oke, T.R., 1987. Boundary layer climates. Second edition. Routledge, London, UK. 435 pp.

Orchard, V.A. and Cook, F.J., 1983. Relationship between soil respiration and soil moisture. Soil Biol. Biochem., 15: 447-453.

Pajari, B., 1995. Soil respiration in a poor upland site of Scots pine stand subjected to elevated temperatures and atmospheric carbon concentration. Plant and Soil, 168-169: 563-570.

Parton, W.J. and Rasmussen, P.E., 1994. Long-term effects of crop management in Wheat-Fallow: II. CENTURY model simulations. Soil Sci. Soc. Am. J., 58: 530-536.

Parton, W.J., Sanford, R.L., Sanchez, P.A., Stewart, W.B., Bonde, T.A., Crosley, D., Veen, H.V. and Yost, R., 1989. Modelling soil organic matter dynamics in tropical soil. In: Coleman, D.C., Oades, J.M. and Uehara, G., (Editors). Dynamics of soil organic matter in tropical ecosystems. University of Hawaii Press, Honolulu, Hawaii, pp. 153-171.

Parton, W.J., Schimel, D.S., Cole, C.V. and Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains Grasslands. Soil Sci. Soc. Am. J., 51: 1173-1179.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.-C., Seastedt, T., Moya, E.G., Kamnalrut, A. and Kinamario, J.I., 1993. Observations and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochem. Cycles, 7: 785-809.

Parton, W.J., Stewart, J.W.B. and Cole, C.V., 1988. Dynamics of C, N, S, and P in grassland soils: A model. Biogeochem., 5: 109-131.

Pastor, J. and Post, W.M., 1988. Response of northern forests to CO_2-induced climatic change. Nature, 334: 55-58.

Paustián, K. and Schnurer, J., 1987. Fungal growth response to carbon and nitrogen limitation: application of a model to laboratory and field data. Soil Biol. Biochem., 19: 621-629.

Peng, C., Apps, M.J., Price, D.T., Nalder, I.A. and Halliwell, D., 1998. Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada: 1. Model testing. Global Biogeochem. Cycles, 12(2): 381-392.

Persson, H.Å., 1983. The distribution and productivity of fine roots in boreal forests. Plant And Soil, 71: 87-101.

Peterson, E.B. and Peterson, N.M., 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. Spec. Rep. 1. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta.

Pietikainen, J., Vaijarvi, E., Ilvesniemi, H., Fritze, H. and Westman, C.J., 1999. Carbon storage of microbes and roots and the flux of CO_2 across a moisture gradient. Can. J. For. Res., 29(8): 1197-1203.

Post, W.M. and Pastor, J., 1996. Linkages - an individual-based forest ecosystem model. Clim. Change, 34(2): 253-261.

Prescott, C., 1996. Influence of forest floor type on rates of litter decomposition in microcosms. Soil Biol. Biochem., 28: 1319-1325.

Press, W.H., Flannery, H.P., Teukolsky, S.A. and Vetterling, W.T., 1986. Numerical Recipes. Cambridge University Press, Cambridge. 818 pp.

Price, D.T., Halliwell, D.H., Apps, M.J. and Peng, C.H., 1999. Adapting a patch model to simulate the sensitivity of Central-Canadian boreal ecosystems to climate variability. J. Biogeogr., 26: 1101-1113.

Priestly, C.H.B. and Taylor, R.J., 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. Monthly Weather Review, 100: 81-93.

Quintilio, E., Alexander, M.E. and Ponto, R.L., 1991. Spring fires in a semimature trembling aspen stand in central Alberta. Inf. Rep. NOR-X-323. Can. For. Serv., Edmonton, Alberta, Canada.

Roussopoulos, P.J. and Loomis, R.M., 1979. Weights and dimensional properties of shrubs and small trees of the Great Lakes conifer forest. Res. Pap. NC-178. USDA For. Serv., North Central Forest Experimental Station, St. Paul, Minnesota.

Ruark, G.A. and Bockheim, J.G., 1987. Below-ground biomass of 10-, 20-, and 32- year-old *Populus tremuloides* in Wisconsin. Pedobiologia, 30: 207-217.

Ruess, R.W., van Cleve, K., Yarie, J. and Viereck, L.A., 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Can. J. For. Res., 26(8): 1326-1336.

Russell, C.A. and Voroney, R.P., 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. Can. J. Soil Sci., 78(2): 301-310.

Saugier, B., Granier, A., Pontailler, J.Y., Dufrene, E. and Baldocki, D.D., 1997. Transpiration of boreal pine forest measured by branch bag, sap flow and micrometeorological methods. Tree Physiol., 17: 511-519.

Sawamoto, T., Hatano, R., Yajima, T., Takahashi, K. and Isaev, A.P., 2000. Soil respiration in Siberian Taiga ecosystems with different histories of forest fire. Soil Sci. Plant Nutr., 46(1): 31-42.

Schlentner, R.E. and van Cleve, K., 1984. Relationships between CO-2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. Can. J. For. Res., 15: 97-106.

Schoette, A.W., 1990. The interaction between leaf longevity and shoot growth and foliar biomass per shoot in *Pinus contorta* at two elevations. Tree Physiol., 7(1/4): 209-214.

Schulze, E.D., Lloyd, J., Kelliher, F.M., Wirth, C., Rebmann, C., Luhker, B., Mund, M., Knohl, A., Milyukova, I.M., Schulze, W., Ziegler, W., Varlagin, A.B., Sogachev, A.F., Valentini, R., Dore, S., Grigoriev, S., Kolle, O., Panfyorov, M.I., Tchebakova, N. and Vygodskaya, N.N., 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink -- a synthesis. Global Change Biol., 5(6): 703-722.

Seastedt, T.R., Coxwell, C.C., Ojima, D.S. and Parton, W.J., 1994. Controls of plant and soil carbon in a semihumid temperate grassland. Ecol. Appl., 4: 344-353.

Sellers, P.J., Hall, F.G., Kelly, R.D., Black, A., Baldocchi, D., Berry, J., Ryan, M., Ranson, K.J., Crill, P.M., Lettenmaier, D.P., Margolis, H., Cihlar, J., Newcomer, J., Fitzjarrald, D., Jarvis, P.G., Gower, S.T., Halliwell, D., Williams, D., Goodison, B., Wickland, D.E. and Guertin, F.E., 1997. BOREAS in 1997: Experiment overview, scientific results, and future directions. J. Geophy. Res., 102(D24): 28731-28769.

Siltanen, R.M., Apps, M.J., Zoltai, S.C., Mair, R.M. and Strong, W.L., 1997. A soil profile and organic carbon data base for Canadian forest and tundra mineral soils. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta, Canada. 50 pp.

Smith, P., Smith, J.U., Powlson, D.S., McGill, W.B., Arah, J.R.M., Chertov, O.G., Coleman, K., Franko, U., Frolking, S., Jenkinson, D.S., Jensen, L.S., Kelly, R.H., Klein-Gunnewiek, H., Komarov, A.S., Li, C., Molina, J.A.E., Mueller, T., Parton, W.J., Thronley, J.H.M. and Whitmore, A.P., 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. Geoderma, 81: 153-225.

Sørensen, L.H., 1981. Carbon-nitrogen relationships during the humidification of cellulose in soils containing different amounts of clay. Soil Biol. Biochem., 13: 313-321.

SPSS Inc., 1996. SPSS Advanced Statistics 7.0 Update. SPSS Inc., Chicago, Illinois. 166 pp.

Steele, S.S., Gower, S.T., Vogel, J.G. and Norman, J.M., 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol., 17: 577-587.

Stottlemyer, R. and Toczydlowski, D., 1999. Nitrogen mineralization in a mature boreal forest, Isle Royale, Michigan. J. Environ. Qual., 28(2): 709-720.

Striegl, R.G. and Wickland, K.P., 1998. Effects of a clear-cut harvest on soil respiration in a jack pine - lichen woodland. Can. J. For. Res., 28(4): 534-539.

Strong, W.L. and La Roi, G.H., 1983a. Root system morphology of common boreal forest trees in Alberta. Can. J. For. Res., 13: 1164-1173.

Strong, W.L. and La Roi, G.H., 1983b. Rooting depths and successional development of selected boreal forest communities. Can. J. For. Res., 13: 577-588.

Taylor, B.R. and Parkinson, D., 1988. Respiration and moss loss rates of aspen and pine leaf litter decaying in laboratory microcosms. Can. J. Bot., 66: 1948-1959.

Taylor, B.R., Prescott, C.E., Parsons, W.J.F. and Parkinson, D., 1991. Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Can. J. Bot., 69: 2242-2250.

Thompson, I.D., Flannigan, M.D., Wotton, B.M. and Suffling, R., 1998. The effects of climate change on landscape diversity: An example in Ontario forests. Environ. Monit. Assess., 49(2-3): 213-233.

Tierney, G.L. and Fahey, T.J., 2001. Evaluating minirhizotron estimates of fine root longevity and production in the forest floor of a temperate broadleaf forest. Plant And Soil, 229(2): 167-176.

Townsend, A.R., Vitousek, P.M. and Trumbore, S.E., 1995. Soil organic matter dynamics along gradients in temperature and land use on the Island of Hawaii. Ecology, 76: 721-733.

Trofymow, J.A., Preston, C.M. and Prescott, C.E., 1995. Litter quality and its potential effect on decay rates of materials from Candian forests. Water, Air, Soil Pollut., 82: 215-226.

Trumbore, S.E., 1993. Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. Global Biogeochem. Cycles, 7: 275-290.

Tryon, P.R. and Chapin III, F.S., 1983. Temperature control over root growth and root biomass in the taiga forest trees. Can. J. For. Res., 13: 827-833.

Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Gudmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncreiff, J., Montagnani, L., Minerbi, S. and Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature, 404: 861-865.

van Cleve, K., Olivier, L., Schlentner, R., Viereck, L.A. and Dyrness, C.T., 1983. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res., 13: 747-766.

van Cleve, K. and Yarie, J., 1986. Interaction of temperature, moisture and soil chemistry in controlling nutrient cycling and ecosystem development in the Taiga of Alaska. In: van Cleve, K., Chapin III, F.S., Flanagan, P.W., Viereck, L.A. and Dyrness., C.T., (Editors). Forest Ecosystems in the Alaskan Taiga: a Synthesis of Structure and Function. Springer-Verlag, New York, pp. 160-189.

Venalainen, A., Tuomenvirta, H., Heikinheimo, M., Kellomaki, S., Peltola, H., Strandman, H. and Vaisanen, H., 2001. Impact of climate change on soil frost under snow cover in a forested landscape. Clim. Res., 17(1): 63-72.

Vitousek, P.M., Turner, D.R., Parton, W.J. and Sanford, R.L., 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: Patterns, mechanisms, and models. Ecology, 75(2): 418-429.

Vogel, J.G. and Gower, S.T., 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. Ecosystems, 1(4): 386-400.

Weber, M.G., 1987. Decomposition, litter fall, and forest floor nutrient dynamics in relation to fire in eastern Ontario jack pine ecosystems. Can. J. For. Res., 17: 1496-1506.

Weber, M.G., 1988. Fire and ecosystem dynamics in eastern Canadian *Pinus banksiana* forests. In: Verhoeven, J.T.A., Heil, G.W. and Werger, M.J.A., (Editors). Vegetation Structure in Relation to Carbon and Nutrient Economy. SPB Academic Publishing, The Hague, Netherlands. pp. 93-105.

Weber, M.G., 1990. Forest soil respiration after cutting and burning in immature aspen ecosystems. For. Ecol. Man., 31: 1-14.

Weber, M.G. and Flannigan, M.D., 1997. Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. Environ. Rev., 5: 145-166.

Weber, M.G. and van Cleve, K., 1981. Nitrogen dynamics in the forest floor of interior Alaska black spruce ecosystems. Can. J. For. Res., 11: 743-751.

Wei, X. and Kimmins, J.P., 1998. Asymbiotic nitrogen fixation in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. For. Ecol. Man., 109(1-3): 343-353.

Wein, R.W., 1990. The importance of wildfire to climate change - hypotheses for the taiga. In: Goldammer, J.G. and Jenkins, M.V., (Editors). Fire in Ecosystem Dynamics: Mediterranean and northern perspectives. SPB Academic Publishing, The Hague, The Netherlands, pp. 185-190.

Westoby, M., 1984. The self-thinning rule. Adv. Ecol. Res., 14: 167-225.

Widen, B. and Majdi, H., 2001. Soil CO_2 efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. Can. J. For. Res., 31(5): 789-796.

Woodwell, G.M., Mackenzie, F.T., Houghton, R.A., Apps, M., Gorham, E. and Davidson, E., 1998. Biotic feedbacks in the warming of the earth. Clim. Change, 40(3-4): 495-518.

Yarie, J., Pulliam, W., van Cleve, K. and Schlenter, R., 1995. Carbon and nutrient availability effect on plant nutrient supply for upland forest sites in interior Alaska. N. Z. J. For. Res., 24(2/3): 234-252.

Curriculum Vitae

7

IAN A. NALDER, Dip. Comm. Eng., ARMIT, B.Sc.(Hon.), PhD Candidate

47 Louisa Lawson Crescent
Gilmore, ACT, 2905
Australia

Telephone: +61 2 6292-3377
E-mail: inalder@gpu.srv.ualberta.ca

FORMAL EDUCATION

Ph.D. Candidate, University of Alberta, Edmonton, Canada.
B.Sc. (Hon.) (1994), Carleton University, Ottawa, Ontario, Canada.
Dip. Comm. Eng. (1968), Royal Melbourne Institute of Technology, Melbourne, Australia.

AWARDS

- John and Patricia Schlosser Environmental Scholarship, University of Alberta (1999).
- Natural Sciences and Engineering Research Council of Canada NSERC67 Graduate Scholarship (1994-1998).
- Walter H. Johns Graduate Fellowship, University of Alberta (1994-1998).
- Canadian Forest Service Graduate supplement (1994-1996).
- Chancellor's Medal, Carleton University (1994).
- Ben and Mary Steinberg Foundation Scholarship, Carleton University (1993).
- Dr. Thomas Betz Memorial Award, Carleton University (1993).
- George Fierheller Scholarship, Carleton University (1992).
- A. Davidson Dunton Scholarship, Carleton University (1991).
- Hewlett-Packard (Canada) Calculator Award, Carleton University (1991).
- Dean's Honours List, Carleton University (1991, 1992, 1993, 1994).

GOALS

Short term: Using my knowledge of forest ecology and models, scientific training, analytical skills and engineering experience, and through collaboration with other researchers, I want to improve the ability to assess the impacts of climate change on forests, particularly the forest floor. This will involve developing more realistic representations of processes in forest models so that litter from all sources and decay rates can be better estimated and models can be quantitatively validated at the stand level.
Long term: Make a significant contribution to our understanding of the terrestrial biotic feedbacks on climate change, and thus provide decision-makers with information necessary to formulate and implement policies that will mitigate the deleterious impacts.

WORK EXPERIENCE

UNIVERSITY OF ALBERTA (EDMONTON, CANADA) **SEP94 – PRESENT**
(EXCL. SICK LEAVE JAN00-JAN02)

Ph.D. studies examining the effect of climate, species and age on forest floor carbon storage in upland areas of the western boreal forest. This involved identification and survey of chronosequences for two contrasting species and three climatic zones, development of a new coring technique and novel method of climate interpolation, extensive investigation of current models and development of a new model to represent and interpret forest floor dynamics. Field work was carried out in Wood Buffalo National Park in Alberta and the Northwest Territories, and across the BOREAS transect in Saskatchewan and Manitoba. **Supervisor**: Dr. Ross W. Wein.

Courses taken and grade points were: Soil Microbiology and Biochemistry (9/9), Forest Soils (9/9), Advanced Fire Ecology (9/9), Research Methods in Forestry (8/9), Agrosystem Simulation (9/9), Plant Stress Physiology (9/9), Communication Research Results (CR).

Under contract to the Canadian Forest Service Fire Group, I undertook the most extensive field survey yet carried out to determine properties of dead and downed wood, analyzed the data, and wrote two major reports as well as two manuscripts which have been published in peer-reviewed literature. This survey across the boreal forests of western Canada will allow for significant improvements in estimating fire fuel loads in this region.

I have co-operated with researchers in the Canadian Forest Service Climate Change Group to validate the CENTURY model on the BOREAS transect and to apply my climate interpolation method to developing gridded climate datasets for Canada.

CARLETON UNIVERSITY (OTTAWA, CANADA) **SEP90 - APR94**

Undergraduate honours degree in Environmental Science, graduating with highest honours and GPA of 11.3/12. My honours thesis integrated GIS biophysical data with a forest gap-dynamics model to examine temporal and spatial vegetation development in Pukaskwa National Park, Ontario.

SELF-EMPLOYED **APR87 - AUG90**

Having achieved my objectives at CMC (see below), I fulfilled a long-term dream by completing a six-month canoe trip across Canada with my wife. This was also an opportunity to explore my developing environmental concerns and to re-assess my career goals. After writing a book about this voyage, I designed and built an “environmentally-friendly” house. With this nearing completion, I took advantage of the new Environmental Science program at Carleton University to expand my knowledge of environmental issues, and equip myself to make a contribution in this field.

CANADIAN MARCONI COMPANY (MONTRÉAL, CANADA) **FEB82 - APR87**

Played a key role in developing CMC's tactical communications products and systems and maintaining their position as a world leader in this field. As a *PROGRAM MANAGER* I was responsible for development of a sophisticated radio system for the U.S. Army from initial marketing through bid preparation to implementation of the 16.5 million dollar contract. As an *R&D MANAGER*, I developed business opportunities for tactical radio products and systems. As *MANAGER, SYSTEMS DEVELOPMENT* I set-up and managed a systems development group to provide the company with a capability of designing, marketing, and producing tactical communications systems. As a *NEW PRODUCTS ENGINEER* I was responsible for identifying, specifying and marketing new products to extend and support the AN/GRC-103 tactical multi-channel radio.

LITTON SYSTEMS CANADA LTD. (TORONTO, CANADA) **JAN81 - JAN82**

AEROSPACE ENGINEER. Responsible for system design and the preparation of technical proposals for various systems including a HF aeronautical communications system, an inter-ship data link system and a battlefield simulator.

RACAL COMMUNICATIONS LTD. (BRACKNELL, UK) **JAN75 - DEC80**

SYSTEMS PLANNING ENGINEER. Carried out system design, proposal preparation and marketing of fixed and transportable communications systems in the MF, HF, VHF and UHF bands for military and civilian customers worldwide. In 1979 the scope of work was expanded to include communications electronic warfare equipment and systems.

ROYAL AUSTRALIAN AIR FORCE **JAN68 - JAN75**

Several positions, including *PROJECT OFFICER* responsible for engineering of all RAAF airfield navigational aids; *RADIO OFFICER* responsible for operation and maintenance of communications and navigational aids at a major RAAF base; proposal evaluation of bids for a transportable radar system; and tactical and strategic communications monitoring involving various operational and engineering positions in a multi-service environment.

OTHER SKILLS

a) Computing and data analysis

- Trained in Algol-80 and have programmed in Fortran, BASIC, VISUAL BASIC and Intel 80x86 assembler.
- Good knowledge of GIS applications, particularly SPANS, IDRISI and Arc-View.
- Good knowledge of SAS and SPSS statistical packages.
- Competent in many DOS and WINDOWS applications.
- Working knowledge of UNIX.

b) Management:

- Strong organizational, communications and project management skills from many years of diverse management experience.

c) Foreign languages:

- French - moderately fluent speaking, reading and writing.

d) Practical:

- Broad range of mechanical, electrical and electronic skills developed in 25 year's experience in engineering and farm upbringing.
- Very competent in field work.

PUBLICATIONS RECORD

MANUSCRIPTS SUBMITTED OR IN PREPARATION

Nalder, I.A., Price, D.T. and Wein, R.W., Can patch models replicate observed stand dynamics?

A test of BORFOR and FORSKA2V in the boreal forests of western Canada. Ecol. Model., Submitted but withdrawn due to sickness. To be resubmitted.

PEER-REVIEWED PUBLICATIONS

Nalder, I.A. and Wein, R.W., 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochem. Cycles, 13(4): 951-968.

Nalder, I.A., Wein, R.W., Alexander, M.E. and de Groot, W.J., 1999. Physical properties of dead and downed round-wood fuels in the boreal forests of western and northern Canada. Int. J. Wildland Fire, 9(2): 85-99.

Nalder, I.A. and Wein, R.W., 1998. A new forest floor corer provides rapid sampling, minimal disturbance and adequate precision. Silva Fennica, 32(4):373-382.

Nalder, I.A. and Wein, R.W., 1998. Spatial interpolation of climatic Normals: test of a new method in the Canadian boreal forest. Agric. For. Meteorol., 92(4):211-225.

Nalder, I.A., Wein, R.W., Alexander, M.E. and de Groot, W.J., 1997. Physical properties of dead and downed round-wood fuels in the boreal forests of Alberta and Northwest Territories. Can. J. For. Res., 27: 1513-1517.

Nalder, I.A. and Merriam, H.G., 1995. Simulating carbon dynamics of the boreal forest in Pukaskwa National Park. Water, Air, Soil Pollut., 82: 283-298.

Nalder, I.A., 1993. Ignoring Limits to Growth. IEEE Technology and Society, 12(3): 24-28.

Grant, R.F. and **Nalder, I.A.**, 2000. Climate change effects on net carbon exchange of a boreal aspen-hazelnut forest: estimates from the ecosystem model ecosys. Global Change Biol., 6: 183-200.

Price, D.T., McKenney, D.W., **Nalder, I.A.**, Hutchinson, M.F. and Kesteven, J.L., 2000. A comparison of two statistical methods for spatial interpolation of Canadian monthly mean climate data. Agric. For. Meteorol., 101: 81-94.

Grant, R.F., Black, T.A., den-Hartog, G., Berry, J.A., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C. and **Nalder, I.A.**, 1999. Diurnal and annual exchanges of mass and energy between an aspen-hazelnut forest and the atmosphere: Testing the mathematical model Ecosys with data from the BOREAS experiment. J. Geophy. Res. (Atm.), 104(D22): 27699-27717.

Peng, C., Apps, M.J., Price, D.T., **Nalder, I.A.** and Halliwell, D., 1998. Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada: I. Model Validation. Global Biogeochem. Cycles, 12(2): 381-392

Brown, S., Shvidenko, A.Z., Galinski, W., Houghton, R.A., Kasischke, E.S., Kauppi, P., Kurz, W.A., **Nalder, I.A.** and Rojkov, V.A., 1996. WG2 Summary: Forests and the global carbon cycle: past, present, and future role. In: Apps, M.J. and Price, D.T., (Editors). Proceedings of the NATO Advanced Research Workshop "The Role of Forest Ecosystems, Forest Management and the Global Carbon Cycle", held at Banff, Canada, September 12-16, 1994. Springer, Berlin, pp. 199-208.

BOOK CHAPTERS

Nalder, I.A., 1996. A forecast of ecological collapse is accurate. In: Cozic, C.P., (Editor). 21st Century Earth: Opposing Viewpoints. Greenhaven Press, CA, pp. 229-235.

CONFERENCE PROCEEDINGS

Price, D.T., **Nalder, I.A.** and Siltanen, R.M., 1998. A 10-km National Climate Surface for Canadian Global Change Studies. Scaling and modelling in forestry: applications in remote sensing and GIS, International Workshop, 19-21 March 1998. Université de Québec à Montréal, Canada,

CONFERENCE PRESENTATIONS

Nalder, I.A. and Wein, R.W., 1999. Carbon dynamics of boreal forests in western Canada: climate change implications. Invited paper presented at the International Symposium on Global Environmental Issues and Forests held at Matsuyama, Japan, April 2/4, 1999.

Nalder, I.A. and Wein, R.W., 1997. Spatial interpolation of climatic Normals in western Canada. Poster presented at the International Boreal Forest Research Association Conference on Disturbance in Boreal Forest Ecosystems: Human Impacts and Natural Processes, August 4-7, 1997, Duluth, Minnesota, USA..

Nalder, I.A. and Merriam, H.G., 1995. Simulating carbon dynamics of the boreal forest in Pukaskwa National Park. Paper presented at International Boreal Forest Research Association Conference on Boreal Forests and Global Change held in Saskatoon, Saskatchewan, Canada, September 25-30, 1994.

Nalder, I.A. 1994. Carbon storage as a state indicator: simulating the dynamics of boreal forests. Poster presented at The First International Symposium on Ecosystem Health & Medicine, June 19-23, 1994, Ottawa, Ontario, Canada.

Nalder, I.A., 1993. Limits to growth and the message for sustainable development. Paper presented at the Institute of Electrical and Electronics Engineers Interdisciplinary Conference "Preparing for a Sustainable Society", June 21/22, 1991, Toronto, Ontario, Canada.